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THE UNIVERSITY OF ALBERTA

A GEOBOTANICAL INVESTIGATION OF THE SUBARCTIC FOREST-TUNDRA
OF THE NORTHWEST TERRITORIES

by

KEVIN P. TIMONEY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

IN

PLANT ECOLOGY

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL 1988

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A GEOBOTANICAL INVESTIGATION OF THE SUBARCTIC FOREST-TUNDRA OF THE NORTHWEST TERRITORIES submitted by KEVIN P. TIMONEY in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in PLANT ECOLOGY.

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ABSTRACT

A geobotanical study of the high subarctic region west of Hudson Bay was undertaken to provide a verifiable and quantitative delimitation of the forest-tundra. Three field seasons of vegetation and landscape studies provided ground truth for a matrix of 1314 National Air Photo Library black and white airphotos. The photos form a grid spanning the forest-tundra, with overlap into the low subarctic and low arctic, from the Yukon--Mackenzie border to the west coast of Hudson Bay.

Airphotos were analyzed for percent cover of nine vegetation--terrain types, occurrence of selected patterned ground features, bedrock and parent materials, landforms, and elevations. Vegetation contour maps and transect diagrams were computer-drawn from percent cover data; occurrence maps of patterned ground features were prepared.

Tree and upland tundra vegetation are discussed in relation to climate, topography, and landscape. The following conclusions were reached:

- 1) The forest-tundra spans an average 150 ± 75 km and on average increases in width from northwest to southeast.
- 2) The predominant pattern of spatial change in tree and upland tundra cover in the forest-tundra is approximated by a sigmoid curve. Gradual change in percent cover at both high and low cover values, and steep gradients in mid-range, are typical.
- 3) Two distinct vegetation--climate--terrain regions are indicated: the Northwest (Mackenzie valley to Coppermine River)

and the Southeast (Great Slave Lake to Hudson Bay). Between these regions, crossover of vegetation and climatic isolines occurs at a major landscape transition north of Great Slave Lake.

4) Highlands account for most southern outliers of forest-tundra in the Northwest.

5) In the Northwest, steep gradients in tree and upland tundra cover usually occur near the northern limit of the forest-tundra; white spruce is the dominant tree. On the acidic terrain of the Southeast, steep vegetation gradients occur near the southern limit of the forest-tundra; black spruce is the dominant tree.

6) The Northwest is colder and receives only about 3/4 the mean annual net radiation available to the Central and Southeast forest-tundra. Edaphic restriction of trees on poor sandy Shield soils, and compensation on higher quality loams in the Northwest may help account for this vegetation--climate anomaly.

PREFACE

As one of the largest relatively undisturbed regions remaining on our planet, the Canadian north presents challenges and opportunities to current and future generations. With the integration of the Canadian north into the global economy, the two prime safeguards of the ecosystem-- low human population density and isolation-- are made irrelevant. We have it in our power, in one generation, to render much of the northland virtually sterile of the more sensitive species of wildlife, and diminished in its capacity to support life-- to create a wilderness in the original sense of the word.

Development must be first and foremost an educational process whose goal is to elevate and encourage human potential and to ensure the integrity of nature's life support systems. Successful resolution of development problems in the Canadian north depends, as elsewhere, upon maintaining perspective when short-term individual, corporate, or local desires conflict with long-term, delayed, indirect, social, and global consequences (Whittaker 1975). The fragile subarctic forest-tundra, or "treeline", can and should be spared the haphazard and senselessly destructive land use that has ravaged much of North America. In the Information Age we can no longer plead ignorance of our actions. While this work is largely an academic endeavor, it is my fervent hope that the baseline data presented, and their interpretations, will prove a useful contribution to our understanding and wise stewardship of the north.

I hope that the interpretations and hypotheses set forth in this dissertation will be challenged and tested, and the results improved upon. If this work inspires or incites others to study and understand the forest-tundra, the labor will have proven a success. Understanding engenders appreciation and respect, and our Canadian north desperately needs respect if it is not to be reduced to a pathetic remnant and a testament of man's spatio-temporal short-sightedness.

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The Computing Services Contingency Fund (University of Alberta) provided a generous allotment of computer funds without which it would have been impossible to complete the computer mapping.

Peter Buttus, senior programmer (Computing Services Dept.), donated much time, effort, and expertise with the nuts and bolts of computer mapping with Surface II.

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extended periods, and donated funds for purchase of 1170 National Air Photo Library prints.

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1 INTRODUCTION

This study delimits and describes quantitatively the high subarctic forest-tundra west of Hudson Bay, with emphasis on the zonal forest and tundra vegetation. The data presented may prove useful as benchmarks in assessing current and future changes in the vegetation cover as a result of climatic change or extensive landscape modification. The data provide a framework in which to study and compare forest-tundra vegetation with applications in bioclimatology, physiology, vegetation dynamics, dendrochronology, paleoecology, and land use planning.

Prior to the study presented here, there had been no comprehensive study of the vegetation and landscapes of the forest-tundra of the NWT. Numerous authors have reported on vegetation, landform, and climate relationships in small or relatively large areas of the subarctic. Differences in aims, terminology, methodology, and interpretation, however, frequently preclude direct comparisons between areas studied by different authors.

Although the "treeline" of the NWT has been mapped by various authors, most of these studies have been based on a minimum of ground and airborne observations. It is often unclear, or left unstated, what data were used and what criteria were applied to delimit the "treeline" or the northern and southern limits of the

forest-tundra. Unfortunately, unverifiable or tentative statements in the literature are interpreted dogmatically by some. The opinion of Tikhomirov (1970:35) illustrates the point:

"The maps of the northern limits of trees have already been made... and there is no need to discuss this problem, for the new data add nothing to the configuration of their areas."

Perhaps a more accurate appraisal of treeline mapping is given by Hustich (1979:210):

"It must be confessed that we use more intuition than precision of concept when we draw our highly interpolated and generalized tree-lines on a map."

The forest-tundra, the "treeline", and the subarctic--arctic boundaries have been defined many times. Mackay (1969) has pointed to the limited value of debating the merits of the various boundary criteria. Those interested in the "Babel of nomenclatures" of subarctic terminology (Hare and Ritchie 1972) should see Blüthgen (1970), Hustich (1966, 1970, 1979), Löve (1970), Ahti (1980), Atkinson (1981), Payette (1983), i.a., and Appendix 7.

Much of the "treeline" literature has been plagued by terminological differences, use of vague or unstated criteria, and excessive extrapolation from locally valid results. In short, criteria should be suited to the objectives, and to the size of the study region. At the subarctic scale, criteria should be functional, simple, observable on airphotos, applicable over a broad geographic region, and independent of local edaphic

conditions. For example, treeless rockland and wetland must be distinguished from climatically controlled upland tundra.

Four vegetation subzones (=regions) were sampled in this study: high boreal, low subarctic, high subarctic, and low arctic (Table 1, Appendix 7). The high boreal closed crown forest region was sampled little; it is characterized by closed crown conifer forest on both upland and lowland mineral soils, and open crown conifer forest over bedrock. Treed peat plateaus and bogs are typical in the lowlands. Mixed-wood forests with aspen and balsam poplar are absent (see Mid Boreal Ecoregion of Bradley et al. 1982), although both species are present as trees.

The transition to the low subarctic open crown forest region is marked by the southern limit of zonal open crown conifer forests on the well-drained mineral soils of uplands. Open crown forest or treeless rockland is found over bedrock; various peat plateaus and palsas are typical.

The high subarctic forest-tundra is defined as the landscape mosaic of zonal tree and tundra vegetation composing a transition region lying poleward of the low subarctic open crown forest region and "southward" of the low arctic tundra region. Its southern limit is defined as the southern limit (<0.1% cover) of upland tundra; its northern limit is defined as the northern limit (<0.1% cover) of trees $\geq 3-4$ m tall. Between these limits, forest and tundra co-dominate in a mosaic with subordinate wetland, shrubland, rockland, burned, and eroding terrain. Forests in the south undergo a transition to single-stemmed and

clonal woodlands, forest-tundras, and thickets in the north. Medium and low shrub tundras are characteristic.

The low arctic tundra is characterized by medium and low shrub, lichen, and tussock tundras, sedge meadows, and peat polygon areas. Its southern limit is marked by the northern limit of trees $\geq 3-4$ m tall. Low and/or prostrate spruce (<3 m tall) are occasional in the low arctic tundra (not readily observable on airphotos). A more complete description of the high boreal to low arctic regions of the NWT is found in Table 1; synonymy and criteria from other studies are given in Appendix 7.

Tree and upland tundra limits applied as cardinal criteria to delimit the forest-tundra in this study are observable on the ground and on black and white airphotos of scale up to 1:70,000. These criteria are widely-applicable due to their simplicity, and their observability on airphotos. Field checking of trees set a minimum height of 3-4 m for the airphoto identification of trees; below 4 m in height, spruce are nearly impossible to distinguish from a dark-toned shrub matrix. The light-toned crowns of larch are locally helpful. Our fieldwork in the NWT indicated that the limit of trees as species (without regard to size) occurred no more than a few km north of the limit of trees $\geq 3-4$ m tall. This contrasts with the observations of Payette (1983) in northern Québec, and J.C. Ritchie (pers. comm.) on the Tuktoyaktuk Peninsula, who found prostrate spruce well north of the limit of arborescent spruce.

The southern limit of upland tundra is locally difficult to discern where: (1) large fires have masked the typical tonal and textural differences between vegetation types (e.g., between Sitidgi and Crossley Lakes east of the Mackenzie River); (2) bedrock-scoured and excessively stony terrain results in edaphic treeless uplands; and (3) lichen and low shrubs on slopes grade from valid upland tundra into the understory of sparse tree communities (common NW of Great Bear Lake). In all such regions, ground truth and/or stereo airphotos are often required.

Other features, such as patterned ground in lake shallows, peatland types, distinctive upland vegetation types, tree canopy closure, and upland and lowland patterned ground, were assessed wherever possible as a check on the primary criteria.

The simple criteria of percent cover of trees and upland tundra apply well for over 95% of the study region. But extensive areas of organic terrain present special problems in the delimitation of the forest-tundra. In the Hudson Bay Lowlands and the Mackenzie Delta proper, tree and upland tundra communities may both be scarce or absent due to excessive soil water, organic soils, or simply to lack of uplands. It might be argued that there is no forest-tundra in the Mackenzie Delta and the Hudson Bay Lowlands. A less physiognomic term than forest-tundra, such as "high subarctic lowlands", is probably more appropriate.

The prime object of this thesis is to provide a verifiable and quantitative delimitation of the subarctic forest-tundra of Canada

west of Hudson Bay. The focus of the thesis is threefold: (1) to describe quantitatively the vegetation cover of the forest-tundra; (2) to identify and interpret vegetation, climate, and terrain relationships within the forest-tundra; (3) to assess the occurrence of landscape features that provide information on terrain and bioclimate. Results of the fieldwork are called upon as needed to elucidate the vegetation gradients, but detailed phytosociology is beyond the scope of the study.

The Results section provides an overview of the vegetation and soils of the study region; describes areal patterns in vegetation cover and selected landscape features; and identifies dominant vegetation communities, associations, and indicator species. In the Discussion, the "present" (circa 1960) vegetation cover is discussed in the context of climate and terrain relationships and historic factors.

Much of the Discussion is based upon correlation of climatic and physical features with vegetation patterns. Such an approach is limited by the dangers inherent in comparison of maps produced by different methods, inaccuracies in mapping, spurious correlations, and the complex interplay of factors that modify surface patterns (such as the masking effect that glacial dispersion may have on the correlation between bedrock type and the mineral composition of the derived soils). For this reason, many of the conclusions must remain tentative while the hypothesized relationships await testing.

2 STUDY REGION

2.1 Physiography

The NW limit of the study region is located at 136°30'W and 70°00'N, west of the Mackenzie Delta, with a SW limit west of Fort McPherson on the east slope of the Richardson Mountains. The study region extends SE to the west coast of Hudson Bay near Eskimo Point, and south to 93°00'W and 58°00'N, south of Cape Churchill, Manitoba. A gazetteer of place names accompanied by a map is provided in Appendix 4A and B.

Physiographic divisions (Geological Survey Canada 1969; Bostock 1976) represented within the study region, proceeding NW to SE, are: Yukon Coastal Plain, Mackenzie Delta, Porcupine Plateau, Richardson Mountains, Peel Plateau, Peel Plain, Anderson Plain, Franklin Mountains, Colville Hills, Horton Plain, Great Bear Plain, Coronation Hills, Bear-Slave Upland, East Arm Hills, Back Lowland, Kazan Upland, Thelon Plain, and Hudson Bay Lowland. By far the largest divisions in the study region are the Kazan Upland and the Bear-Slave Upland.

The following description of physiographic and geological features is modified after Geological Survey of Canada (1968, 1969) and Bostock (1976).

The study region may be divided physiographically and geologically into two great parts: a core of Precambrian (mostly igneous and metamorphic) rocks forming the Shield, and a

surrounding crescent of younger sedimentary rocks forming the Borderlands. About two-thirds of the study region is found within the Shield, and one-third found within the Borderlands.

The surface of the Shield is domed, with a slightly depressed center and an outward shelving rim terminated by a steep edge. The depressed center of the Shield is occupied mainly by flat-lying Paleozoic and Mesozoic sediments. Only Paleozoic sediments reach the study region as Ordovician and Silurian limestones and dolomites. These sediments are mantled by extensive organic terrain and glaciomarine re-worked tills. Post-glacial marine overlap extended as much as 150 km inland, and as high as 205 m above present sea level.

Within the Kazan Region of the Shield there are large areas of flat-lying sandstone and volcanic rocks (Thelon Plain), sediments and diabase sills (East Arm Hills), and complex suites of sedimentary, igneous, and metamorphic rocks (the lower Coppermine River area of the Bear-Slave Upland; Coronation Hills; and the Henik Lakes area of the Kazan Upland).

Younger sedimentary rocks of the Borderlands surround the Shield as two concentric rings. The inner ring is composed of generally flat-lying sedimentary rocks which overlie the shelving rim of the Shield. These flat-lying sediments and their glacially-modified surficial material form the land surface in the northwest of the study region. The outer ring of the Borderlands comprises mountains and plateaus in which the younger rocks are deformed. These deformed rocks lie mostly outside the study region in the Cordillera.

2.1.1 The Shield

The majority of the Shield has been metamorphosed. Archean granitic gneisses comprise most of the bedrock. There are large areas of Archean paragneisses and paraschists, basic and intermediate volcanics and metavolcanics, granites, and Proterozoic sandstones. Relatively large areas of Archean sediments and diabase sills and dykes are found on the East Arm of Great Slave Lake and along the Coppermine River north of Point Lake.

Archean sediments are commonly poorly sorted and consist mostly of greywacke, argillaceous material (e.g., derived slates), arkose sandstone, conglomerate, quartzite, and carbonates. Volcanic rocks of the Shield north of Great Slave Lake are predominantly basaltic. In places they have been metamorphosed to amphibolite and gneiss (Stockwell et al. 1976). Proterozoic sedimentary rocks of the Shield (e.g., the Thelon Plain) are typically better sorted and contain more limestone than Archean sediments (Stockwell et al. 1976).

The surface of the Shield is an ancient erosion surface. In Archean time the Shield was peneplained and partly dissected. During the Proterozoic, the Shield surface was buried and exhumed once or twice, followed in the Paleozoic by a similar burying and exhuming of Paleozoic strata. Finally, the surface was scoured during the Pleistocene. It appears that the Precambrian surface has been little changed since the removal of the Paleozoic cover, and that glaciation has only slightly modified its character.

Seen from a prominent vantage point, the Shield horizon is smooth, and its surface fairly even. Monadnocks and small ranges of hills provide local relief, which seldom exceeds 60-90 m.

Lakes and streams occupy a relatively large portion of the Shield, with cover normally between 10-25% (Figure 8A). The overall pattern of streams and lakes is controlled by bedrock structure. Stream channels and lakes commonly occupy fracture zones, major joints, or traces of soft strata. Trellis drainage patterns may develop where streams follow straight lineaments, or major fractures and joint systems in massive rocks. In areas of the Shield where glacial deposition is prominent, stream patterns are controlled by drumlin fields, drumlinoid ridges, and ribbed moraine (e.g., west of Boyd Lake on the Dubawnt River). The largest lakes in the study region, Great Bear and Great Slave Lakes, occupy the rim of the Shield, where Archean and Proterozoic Shield rocks to the east abut with Paleozoic and Mesozoic sediments to the west.

2.1.2 The Borderlands

The Borderlands are represented by five main physiographic divisions. A brief description of these divisions follows.

Horton and Anderson Plains. These lie north and NW of Great Bear Lake and form the Arctic Slope where drainage is directly to the Arctic Ocean. The Anderson Plain is covered by a sheet of glacial till and outwash, whereas the slightly higher Horton Plain

is only thinly covered in till. The southern parts of both areas are underlain by Ordovician-Silurian and middle Devonian dolomites and limestones. The SW portion of the Anderson Plain is underlain by upper Devonian non-marine sandstones and shales. The northern portions of both areas are underlain by Cretaceous shales, siltstones, and mudstones. Much of the western part of the Horton Plain is rocky; in the eastern parts, rolling areas of till occur; lakes are small and scattered. The Anderson Plain is slightly undulating, and large parts of its higher levels are rocky. There are extensive areas of outwash and associated meltwater channels. In both areas, streams are entrenched 30-120 m below the plain.

Colville Hills. This division is located NW of Smith Arm, Great Bear Lake. Here Ordovician-Silurian and middle Devonian carbonates and shales project 300 m above the surrounding plains and reach elevations up to 675 m ASL. The hills and ridges enclose several large lakes (Colville, Maunoir, Aubry, des Bois, and Belot).

Great Bear Plain. This division is underlain by lower Cretaceous shales, with smaller amounts of Ordovician-Silurian carbonates and related rocks east of McVicar Arm and non-marine sandstone and related rocks on Cape MacDonnel. Its surface lies usually below 300 m ASL, but the Scented Grass Hills and Grizzly Bear Mountain reach elevations of about 450 m.

Mackenzie Delta. This division presents a complex surface of Tertiary and Quaternary sediments and includes not only the present delta, but remnants of former delta and fluvial and marine

deposits which collectively form the present Arctic Coastal Plain. The delta plain features numerous lakes and channels, and, in older parts of the delta, many pingos.

2.2 Till

Over 99% of the study region was glaciated during the Pleistocene. Only a small area between the lower Anderson and Horton Rivers seems to have escaped glaciation (Zoltai et al. 1979).

Retreat of the Laurentide Ice Sheet proceeded generally west to east across the study region. Deglaciation occurred first in the northwest, beginning 14 KBP in the lower Mackenzie valley, and reached the central district north of Great Slave Lake by 10 KBP (Dyke and Prest 1987). By 8.4 KBP, only Keewatin and the southeast corner of the Mackenzie District (Dubawnt River--Kasba Lake area) remained ice-covered. Deglaciation of the study region was essentially complete by 7.8 KBP, with a remnant of the ice sheet centered on Yathkyed Lake and the lower Kazan River (Dyke and Prest 1987).

The glacial deposits of the study region are late Wisconsinan in age, and till comprises about 75% of these deposits. Even in many areas subjected to glacial or post-glacial marine or lacustrine inundation, the predominant surficial material is till (e.g., the Dubawnt River; cf. Geological Survey Canada 1967).

Scott (1976) divided Canada into seven till provinces, and the following description is modified after his overview. Three of the seven till provinces, the Prairie-Mackenzie, the Canadian Shield, and a small segment of the Hudson Bay province, lie in the study region. A short description follows.

Tills of the Prairie-Mackenzie province are found in the northwest of the study region. Their lithology falls into two main types: weak and generally poorly-consolidated shale, siltstone, and sandstone; and better-consolidated carbonate and related Paleozoic rocks. Paleozoic rocks are widespread along the interface of this province and the Shield. Underlying bedrock has supplied >80% of the bulk of the tills in the region.

Thickness of Prairie-Mackenzie tills varies. The thickest tills are often composed of several till sheets each derived from separate glaciations. Thin till is found over much of the Horton Plain. A typical texture is loam to clay loam. The clay component, which contains much montmorillonite derived from bentonitic shales, makes the tills sticky when wet, and of low permeability.

Tills of the Canadian Shield are complex in lithology. Parent materials are largely granitic gneisses, sediments, metasediments, basic and intermediate volcanics and metavolcanics, and granites. Till thickness is generally 2-8 m, being thicker in bedrock valleys. Till is thin, patchy, and weathered over an area of polished and striated bedrock terrain lying along the western rim of the Shield between Great Slave Lake and McTavish Arm of Great Bear Lake. The vicinity of the Coppermine River valley is much

less rocky, but east of the Coppermine, from the Hood River south to Lac de Gras, there are large areas of scoured bedrock. The bold bluffs of the East Arm of Great Slave Lake, much of the land to the south and north of the East Arm, the area NE of Clinton-Colden Lake, and that ENE of Lake Athabasca also present much bare bedrock and scoured terrain.

The mineralogy of Shield tills is as complex as their lithology. Shield tills are most often non-calcareous. Clay mineralogy is complex with kaolinite as a prominent component. They are typically coarse-grained, with low clay content. Soils derived from granitic rocks are of sandy loam and loamy sand texture. Soils derived from glaciofluvial, fluvial, and ice contact materials are often of sandy loam, sand, or gravel texture (Bradley et al. 1982; this study).

Red tills are found in central Keewatin and adjacent eastern Mackenzie District where red beds of the Dubawnt Group have been eroded and dispersed in all directions from the vicinity of the Keewatin ice divide (Scott 1976).

Tills in the NW portion of the Hudson Bay province are variable in lithology, texture, and provenance. In the vicinity of Churchill, Manitoba, there are multiple tills of alternating provenance. Those deposited by SE flowing Keewatin ice are sandy and stony; those deposited by west-flowing ice from east of Hudson Bay are fine-grained, with few stones, and rich in Paleozoic carbonate debris (Dredge 1979; Shilts 1980). These tills are typically buried under peat and blankets of lacustrine and marine silts.

2.3 Soils

Over three-fourths of the soils in the study region are derived from tills. Glaciofluvial, organic, ice contact, alluvial, lacustrine, colluvial, glaciomarine, and aeolian materials are locally important. Organic soils are prevalent on the Arctic Coastal Plain, the Hudson Bay Lowlands, and locally elsewhere. Glaciofluvial soils are widespread, but usually of limited area. Lacustrine deposits and lacustrine re-worked tills are found around Great Slave and Great Bear Lakes, and the Thelon, Dubawnt, and upper Kazan Rivers (Geological Survey Canada 1967; Bradley et al. 1982). Alluvium is important in large river valleys such as the Mackenzie, Coppermine, and Thelon Rivers. Colluvium is found in actively eroding areas with steep topography (Zoltai et al. 1979), e.g., the Smoking Hills of the lower Horton River.

In subarctic and low arctic soils, organic mats where present are usually fibrous. Buried organic matter is widespread and due primarily to cryoturbation. Instability of the soil due to cryoturbation and mass soil movement is widespread. As a result, mature soils that have developed undisturbed over long periods are rare (Ritchie 1984).

Carbon:nitrogen ratios approximate 15:1, and are higher in turfy soils (Tedrow 1977). Fine-textured soils are often massive in structure, but some upper horizons may exhibit granular ("shotty") structure (Tarnocai 1973). Some C horizons, when dry may show poorly-defined blocky structure (Tedrow 1977). The coarser soils of the Shield are structureless (single-grain).

Since leaching is not pronounced, organic acids may accumulate in the upper horizons (Tedrow 1977). It is not uncommon for surface horizons to be as much as 2 pH units lower than the C horizon.

Brunisols, gleysols, and fibric organic cryosols predominate in the low subarctic. In the high subarctic, the increasing prevalence of permafrost places fine-textured and/or poorly-drained gleyed soils into the cryosolic order. Brownish mineral soils in this region may be either brunisols, often of cryoturbic phase, or brunisolic cryosols. In the low arctic, brunisols are rare and the vast majority of soils are cryosols. Rockland is found in all regions wherever <10 cm of soil overlies bedrock. Areas of rockland are most prevalent in the central Mackenzie District north of Great Slave Lake (Figure 9A).

While a great variety of soils is found across the study region, zonal soils fall into two textural categories with characteristic chemical and physical properties (see Results 4.4 and Appendices 3 and 6 for details).

Fine-textured clay loams to loams predominate in the northwest from the Mackenzie valley eastward to the Coppermine River. These soils are typically derived from moderately calcareous tills overlying sedimentary rocks. Median soil acidities range between 5.3-6.2 for mineral horizons (Table 2); cation exchange capacity is high (18.6-26.8 meq/100 g; Table 2), as are total soil nitrogen (0.11-0.13%; Table 3) and available potassium (0.22-0.51 meq/100 g; Table 3).

By virtue of their fine textures, northwest soils have high water-holding capacity and thus freeze slowly in the fall and thaw

late in spring. Low temperatures and permeabilities in these fine-textured soils result in a prevalence of orthic, regosolic, and gleyed cryosols (northward); orthic eutric brunisols and orthic gleysols occur along the southern fringe of the forest-tundra in the northwest.

In comparison, the coarser-textured sandy loams, loamy sands, and sands of the Shield are typically derived from non-calcareous tills overlying crystalline bedrock. Median soil acidities range between 3.9-5.3 for mineral horizons (Table 2); CEC is low (1.5-6.2 meq/100 g; Table 2); both total soil nitrogen (0.01-0.07%; Table 3) and available potassium (0.04-0.07 meq/100 g; Table 3) are also low compared to northwest soils.

The coarser-textured, more freely-drained parent materials of the Shield, together with higher soil temperatures and greater precipitation than that of the northwest, make brunisols the predominant soils of the Shield. Orthic dystric brunisols (often of cryoturbic phase) predominate in the southern portion of the forest-tundra (with some orthic eutric brunisols), giving way to brunisolic and regosolic cryosols northward. Orthic humic gleysols (southward) and gleysolic cryosols (northward) occur in poorly-drained areas. Eutric brunisols are apparently rare in Keewatin.

2.4 Patterned Ground and Permafrost

Circles (including mudboils) and net patterns are widespread on

Shield tills. Due to abundant circles and nets, some areas of the high subarctic and low arctic have a freckled appearance on black and white airphotos. Upland polygons are found occasionally in tills, but are most typical of sand deposits.

Patterned ground in lake shallows is present across much of the subarctic and abundant in the low arctic (this study). This subaqueous patterned ground is most easily observed where boulders have been sorted into troughs, forming an obvious pattern visible on airphotos.

Extensive areas of loamy soils in the subarctic and low arctic are covered with earth hummocks (=non-sorted nets). About 75% of the northern Mackenzie River area has hummocky microrelief (Zoltai and Pettapiece 1974). These hummocks are about 1-2 m in diameter and 20-80 cm high (Zoltai and Pettapiece 1974), and are difficult to discern on airphotos unless the forest is sparse and the hummocks large and lichen-topped. Where ice-rich fine-textured slopes are seasonally saturated with meltwater, runnels (also termed rillwork stripes, horsehair drainage; (Washburn 1973)) are abundant (airphoto observ.).

Although the precise climatic and site requirements for patterned ground have not been identified, the southern limit of active and large-scale features (observable on airphotos) has been suggested to coincide with the -4°C mean annual air isotherm (Bird 1967). This translates to a mean annual soil temperature of about -0.5°C (using the adjustment of $+3.5^{\circ}\text{C}$ from mean annual air to soil temperature in Brown 1970).

Whether the "conspicuous" patterned ground of Bird (1967) includes peatland polygons is not specified. Patterned ground observable on airphotos extends southward into the open crown forest region in two forms, or three forms if "patterned ground" is defined broadly: peatland polygons, upland equiforms, and slope runnels (see section 4.2).

Brown (1970) placed the southern limit of permafrost at a mean annual air isotherm of -1°C . Between -1 and -3.5°C , permafrost is discontinuous, occurring primarily in dry peats, and also some north-facing slopes and shaded areas. The widespread zone, where permafrost is present in most terrain, corresponds to a mean annual air temperature of -3.5 to -8.5°C (0 to -5°C soil (Brown 1970)). Below -8.5°C mean annual air temperature, permafrost is continuous.

2.5 Climate

While climate is a cardinal factor in the the zonation of biomes, detailed local or regional correlations of climate and vegetation are not now possible for the study region. Available climatic maps provide continental and sub-continental scale patterns, and are prepared by interpolation from widely-spaced synoptic stations, plus a few local temperature and precipitation data (F.K. Hare, pers. comm.). The accuracies of isolines on these synoptic maps vary. Hare (pers. comm.) estimates the

accuracy of synoptic climatic maps for Canada to be a few tens of km, at best, to even a few hundreds of km for the arctic. Temperature-related data may be accurate to within $\pm 0.5^\circ$ latitude (± 55 km); the amount of smoothing used in drawing isotherms is also important to consider (R.G. Barry, pers. comm.). Maps of frost-free period, snow cover disappearance, etc., may be accurate to $\pm 1^\circ$ latitude (Barry, pers. comm.).

The median summer position of the Arctic Front has been widely referenced as a correlate of "treeline" (cf. Bryson 1966; Barry 1967; Hare 1968 for seminal papers). Yet the Arctic Front is difficult to define, and at most times there is no sharp boundary between Arctic and Pacific air; at ground level, its statistical position is an extreme approximation (Hare, pers. comm.). Its depiction is perhaps accurate to about $1-2^\circ$ latitude (Barry, pers. comm.). The Arctic Front is a broad transition zone, even east of the Mackenzie River, where the line is sharpest (Hare, pers. comm.). On the average, fairly warm and moist Pacific air predominates to the west of this zone, and cold Arctic air predominates on the ground to the east (Hare, pers. comm.). Arctic airstreams dominate the forest-tundra for 11-12 months of the year (Bryson and Hare 1974).

The climatic description that follows is based primarily on comparison of the forest-tundra region (as delimited in this study) with the climatic maps of Hare and Hay (1974). The subarctic forest-tundra of Canada west of Hudson Bay lies between the July isotherms of $10-13^\circ\text{C}$, and mostly within the July mean isotherms of 7.0 and 4.5°C at the 850 mbar level (about 1.5 km

aloft). Most of the forest-tundra lies within a zone of maximum standard deviation (1.5 C) of July mean monthly temperature.

Mean annual air temperature for the forest-tundra lies between -10 and -6.5 C east of Great Bear Lake, and between -10.5 and -9 C westward to the Mackenzie Delta (Fletcher and Young 1978). Mean daily air temperatures for the forest-tundra rise to 0 C by about 7-31 May, with the 0 threshold reached earliest in central districts (NE of Yellowknife and SE of the East Arm of Great Slave Lake). Mean daily air temperature falls to 0 C by about 1 October for much of the forest-tundra with the northwest sector cooling about one week earlier and the central sector cooling to 0 C about one week later.

Frost-free period ranges from 50-80 days, with the fewest frost-free days found to the north and NW of Great Bear Lake. Frost-free period at ground level may be only half that of the air; for subarctic Siberia, frost-free period for the air is 60-90 days, but only 30-60 days at ground level (Dolgin 1970). Forest-tundra plants must thus be adapted not only to a short frost-free season, but also to occasional frosts during the growing season.

Most of the land from the Yukon border to the East Arm of Great Slave Lake is essentially snowfree by 15-31 May. Eastward, snowmelt averages about a week later, with northern Manitoba and southern Keewatin becoming nearly snowfree between about 21 May and 7 June. Snow patches may persist throughout the summer locally in the north (field observ.). In contrast, most of the closed-crown boreal forest of western Canada is snowfree by 15

May; and more importantly, this snow lies concealed beneath the forest canopy. The low spring albedo (about 0.1-0.3) of the closed-crown forest canopy allows far more rapid spring warming than over tundra (Hare and Ritchie 1972; Hare and Thomas 1979). The closed-crown forest consequently has a much longer frost-free period of 70-100 days. The duration of the thaw season (total days reaching $>0^{\circ}\text{C}$) for the forest-tundra lies between 90-150 days, whereas for the closed-crown forest the thaw season is approximately 150-200 days (Hare and Thomas 1979).

The persistence of lake ice is related both to climate and to size of lake. Small lakes at the southern limit of the forest-tundra may be ice-free by 15 June; large lakes near the limit of trees may remain largely ice-covered till 15 July, and even into August (Fisheries and Environment Canada 1978; field observ.). The East Arm of Great Slave Lake has a depressing effect on spring temperatures; its waters are usually not clear of ice until 1 July (Bradley et al. 1982). Great Bear Lake is a similar cold spot; ice-out does not normally occur before 1 July (Fisheries and Environment Canada 1978). Lake freeze-over occurs in the northwest about 5 October, and in the southeast about 20 October. Great Bear and Great Slave Lakes freeze much later, Great Bear by 15 November, and Great Slave about 1 December (Fisheries and Environment Canada 1978).

Measured values for rain and especially snowfall in the subarctic are probably underestimates on the order of 10-50% (Hare 1971). Mean annual measured precipitation is light, ranging from about 25-40 cm in the southeast, to 18-30 cm in the drier

northwest. Greatest measured snowfall is found over southern Keewatin and northern Manitoba, ranging from 80 cm near the limit of trees to 140 cm in the Hudson Bay Lowlands. In the northwest, snowfall peaks in the Mackenzie valley at 140 cm, but in general the area receives between 90-110 cm per yr. Between the NW and SE extremes, the central forest-tundra receives about 100-120 cm snow per yr.

Thunderstorms (measured) are rare in the forest-tundra, averaging five or fewer per year in the south and one or none in the northwest. However, Rowe et al. (1975) caution that local topography and relief can deflect air masses, encouraging local convectional instability and thus lightning. As a result, thunderstorms may be more common than the data indicate.

Winds are probably strongest over Keewatin and northern Manitoba, but data are too sparse to provide accurate values.

3 METHODS

3.1 Field Methods

Field studies were conducted during the summers of 1982-84. Travel was by canoe across and along the forest-tundra transition. The prime objective of the field studies was to provide ground truth for airphoto interpretation. Three sampling methods were employed: (1) Stands provided the most detailed ecological data, and were concentrated in the uplands. (2) Special transects were conducted to augment tree growth data gathered in the stands. (3) Relevés were concentrated in the lowlands.

Nomenclature for mosses follows Ireland et al. (1980), except for *Dicranum* where Peterson (1979) was followed; for liverworts, see Schuster (1966, 1969, 1974, 1980); and for lichens, Thomson (1979, 1984). Scientific and common names of vascular plants follow Porsild and Cody (1980).

Tree, upland tundra, and tall shrub communities were studied using stands. Straight-line transects were run through representative vegetation, along which 30-70 quadrats were placed randomly. Species presence and percent cover were estimated for non-tree species using 0.25 sq m quadrats.

Four size classes of trees were defined: a) trees, with dbh $\geq$ 10 cm; b) saplings, 2.5 cm $\leq$ dbh $<$ 10 cm; c) transgressives, dbh $<$ 2.5 cm, and height $\geq$ 2 dm; d) seedlings, $<$ 2 dm in height, and rooted.

Trees were sampled with 25 sq m circular plots, saplings with 12.5 sq m half circle plots, transgressives with 6.25 sq m quarter circle plots, and seedlings with the 0.25 sq m quadrats used for the ground layer. Presence, density, dbh (dominance), height, cover, and age (increment cores) were determined for trees and saplings. Height was determined with a clinometer, and crown cover was estimated by the average maximum radius of the stem branches. All but age were determined for transgressives and seedlings.

A representative soil pit was analyzed by horizon for thickness, color, texture, structure, consistence, horizon boundary, roots, pH, drainage, and parent material, and nearby vegetation and terrain were described.

Special transects were designed to augment tree data without the use of detailed stands. Species, dbh, height, cover, and age were determined for 10-20 selected trees or saplings. In total for stands and special transects, 1850 tree stems were sampled between Inuvik and the Dubawnt River. In decreasing order of ring-counted specimens, tree species were *Picea mariana*, *P. glauca*, *Betula papyrifera*, *Pinus banksiana* and *Larix laricina*.

Relevés were used primarily in the lowlands. Species presence was noted, and cover classes estimated. An average releve measured 0.1 ha in area.

In addition to stands, special transects, and relevés, landscape photos with extensive notes were taken in the vicinity

of study areas, and during travel days. Low-level oblique airphotos with notes were taken en route to "put-in" points and returning from "take-out" points.

Altogether, 84 stands, 43 special transects, and 27 releves were studied, and 1600 slides and photos were taken (see Figure 2).

Ground truth studies were augmented by reference to published landscape, vegetation, and soil studies. An additional 100 color slides with notes were provided by people who have studied or travelled through the subarctic and low arctic. Figure 2 details the location and sources of ground truth information.

3.2 Laboratory Methods

A matrix of National Air Photo Library black and white photos was established; airphotos were taken between 1952 and 1979, with most taken prior to 1960 (Figure 1). Although the imagery is dated, the quality is good. As climatic--vegetation comparisons comprise an integral part of this study, the climatic normal period is relevant: many climatic data and their derived maps are based upon the 1931-60 normal period, while global and net radiation are based on either the 1957-65 or 1957-64 period. Fortunately, most of the airphotos were taken either near the end or the midpoint of the climatic normal period.

To ensure that outliers of forest-tundra were not overlooked, the airphoto matrix extended from the low subarctic to the low

arctic. Airphotos were analyzed at 6X magnification with a stereo-microscope. The following information was gathered from each photo:

(a) percent cover of tree, upland tundra, shrubland, treeless wetland, and burned forest vegetation types was estimated visually, as was percent cover of rockland, eroding terrain, water, and unsuitable (due to focus, clouds, etc.); notes accompanied each category; see Appendix 1 for a key to physiognomic vegetation types;

(b) vegetation region (using presence/absence of tree and upland tundra vegetation, and the landscape criteria given in Table 1);

(c) the presence or absence of upland patterned ground, sorted nets and stripes in lake shallows, peatland polygons, and stripes and runnels on slopes;

(d) prominent surficial features such as parent material, glacial landforms, badland topography, beaded streams, rilled peat plateaus;

(e) the longitude and latitude of the center of each photo;

(f) mean, maximum, and minimum elevation and relief were estimated by plotting the photo on a 1:250,000 NTS topographic map;

(g) bedrock type was determined by reference to Geological Survey of Canada maps and publications, or other reports;

(h) physiographic division (Bostock 1976).

Airphoto cover percentages were adjusted to percent of land

surface by algorithms correcting for percent water and unsuitable. Photo positions were transformed to a Lambert Conformal map projection, and the airphoto cover data were then passed to Surface II. Appendix 2 details the calculations.

Surface II software (Sampson 1978) was used to generate 360 X 180 grid matrices, from which averaged and smoothed contour maps and transect diagrams were drawn. In order to show local detail, averaging was generally kept to a minimum (4-6 photos), and a distance-weighted function of $1 * D^{-6}$ was used to minimize the effect of neighbor photos upon a sample grid point. In the map-transformed 3-dimensional transect diagrams, the height above the plane is proportional to percent cover; the compass arrow is plotted on the central meridian (114°45'W); the limits of the airphoto data are marked by a vertical "cliff" which is distinct from genuine changes in percent cover within the study region.

In smoothed depictions of upland tundra and tree cover, the data have been generalized by distance-weighted averaging with 12 neighbors, rather than 4-6. In such a smoothed depiction, the value of a contour line loses its local accuracy and instead takes on regional and synoptic relevance.

Lambert conformal maps showing the occurrence of upland patterned ground, sorted nets and stripes in lake shallows, peatland polygons, and stripes and runnels were produced using *APLOT and *PLOTLIB (University of Alberta, Computing Services). Draft maps (not presented) of elevation, relief, bedrock type and hardness, and sedimentary vs. non-sedimentary terrain were similarly prepared to aid in interpreting the vegetation patterns.

Contour and occurrence maps were overlaid onto a World Data Bank II (University of Alberta) topographic map. A first approximation of the forest-tundra was thus completed for the study region using a matrix of 1130 photos. Maps were then scrutinized and unusual patterns highlighted. Airphotos in questionable areas were re-analyzed.

Because the contour lines are drawn from averaged data, steep gradients in tree and upland tundra cover cause contour lines to be drawn north or south of their true positions. For example, the typical steep rise in upland tundra cover at the southern limit of the forest-tundra in the southeast tends to push an averaged contour southward. On draft maps this artifact was assessed against ground level information and non-averaged airphoto data. Departures from "true" position were minimized by increasing the density of airphotos in areas of steep gradients.

An additional 184 airphotos located in areas of rapid vegetation change, low photo density, and areas covered by poor quality photos, were analyzed and incorporated into the final matrix of 1314 photos, and maps were re-drawn as above. Correcting for the small amount of stereo overlap, the airphotos cover about 260,000 sq km, or circa 24% of the the study region.

A certain portion of every photo cannot be analyzed due to poor photo quality. Focus is the prime reason for poor quality, and this problem is most serious at photo edges. Figure 3A depicts the percent cover of unsuitable image due to focus, clouds, and overwriting. In the photos sampled, unsuitable usually ranged from 2-10%. Locally, such as NE of the Colville Lakes, the

vicinity of Great Bear Lake, north of Courageous Lake and east of Point Lake, and east of Eyeberry Lake on the Thelon River, unsuitable reached 25%. Beyond 25% unsuitable, overall photo quality was often too poor to permit analysis; such photos were rejected and replaced by photos of a different edition.

Figure 2 depicts sources of ground information used in the study. The large boxes enclose areas studied by other workers; reference numbers are listed down the right side of each box. These studies contained ground and/or low-level photos with vegetation descriptions and locations that could be pinpointed and tied to airphotos used in the analyses.

Small boxes with a central vertical line denote areas studied on the ground during the course of this study. Straight lines trace areas flown at low-level during the study. "Tree" symbols denote positions of color slides with vegetation descriptions contributed by other workers.

Checking of the contour maps with airphoto data and ground truth indicates the normal accuracy of the isolines to be ± 15 km. In later drafts of tree and upland tundra cover, data located at distribution limits were increased by duplicating data points with zero values such that averaged contours approximated the "true" position based on unaveraged data. Since the limit of trees can typically be determined with more confidence than the limit of upland tundra, this duplication of data was carried out more vigorously at the northern limit of the forest-tundra. For this reason, the northern limit of trees as depicted approximates the true limit with no detectable error. Eastward from near

longitude 115°W, the southward bias of the limit contour usually lies between 5 and 10 km.

4 RESULTS

To aid the reader in locating geographic areas referred to in the text, a gazetteer of place names (Appendix 4A) and a location map (Appendix 4B, in map pocket) are provided. A synopsis begins each section of Results and Discussion.

Data, results, and interpretations must be placed in the context of their proper space-time scales (see Delcourt et al. 1983 for space-time domains). Ground level sampling applied to the vegetation stand scale (up to 10^4 m^2); ground level photos and observations provided information on scales from 10^1 - 10^6 m^2 ; these ground studies were used in the interpretation of airphotos of scale $\sim 2 \times 10^8 \text{ m}^2$ (vegetation sub-types and types); the airphotos formed the database for the vegetation cover maps which depict the plant cover at the vegetation formation and formation zone scale (10^{12} m^2).

Time scales vary also, but all fall within the temporal micro-scale of Delcourt et al. (1983). Ground studies may detect seasonal and yearly changes in the vegetation (10^{-1} - 10^0 yrs). Airphotos may detect rapid vegetation change in response to fire and human disturbance (10^0 yrs), but in the absence of disturbance and regeneration, airphoto detection of directional

vegetation change probably requires $\geq 5 \times 10^1$ yrs (e.g., Scott et al. 1987a). In the absence of disturbance events, sensitivity to change at the map scale probably requires $\sim 10^2$ yrs due to the smoothing necessary in map production. Under stable climatic conditions vegetation patterns at the airphoto and map scales might persist indefinitely. The degree to which northern vegetation might persist under an unfavorable climate is the topic of debate and research (see sections 5.1, 5.5).

4.1 Overview of vegetation regions

An overview of vegetation subzones in the study region giving characteristic vegetation and landscape features is provided.

Figure 1 (in map pocket) plots the position of sample photos and indicates in what vegetation region (determined by presence/absence of trees and upland tundra and qualitative criteria in Table 1) each photo occurred. Compound regions indicate that characters of more than one vegetation region were present on a given photo. Symbol size in Figure 1 is scaled to one half the terrain coverage of a 1:50,000 scale photo, or one fourth the coverage of a 1:70,000 photo. Vegetation and landscape features characteristic of the vegetation regions are given in Table 1.

Table 1. Overview of vegetation zones and their characteristic vegetation types and landscape features (modified after Bradley et al. 1982).

Closed Crown Forest Region (High Boreal)	
Mineral Terrain:	a) Upland and lowland closed-crown conifer forest (black spruce, white spruce, jack pine, paper birch, <i>Cornus canadensis</i>, <i>Linnaea borealis</i>, <i>Viburnum edule</i>, <i>Hylocomium splendens</i>, <i>Pleurozium schreberi</i>, <i>Ptilium crista-castrensis</i>, and <i>Peltigera aphthosa</i>) b) Open crown forest over bedrock (black spruce, jack pine, +/- paper birch, <i>Cladonia</i>, <i>Stereocaulon</i>)
Organic Terrain:	a) Treed peat plateaus with thermokarst features, palsas and treeless bogs (black spruce, larch, <i>Ledum groenlandicum</i>, <i>Sphagnum</i>, <i>Cladonia</i>) b) Fens and meadows (dwarf birch, <i>Carex</i>, <i>Salix</i>, <i>Campyllum</i>, <i>Calliergon</i>, <i>Drepanocladus</i>, <i>Scorpidium</i>; +/- larch, black spruce)
Patterned Ground and Permafrost:	Earth hummocks on fine-textured soils; sporadic permafrost in peat plateaus, palsas, bogs
Comments:	Northern limit of tree-size <i>Populus</i> spp.; fires frequent, return interval of ≤ 100 yrs; wide mats of shoreline aquatic vegetation; this region sampled little in this study
Open Crown Forest Region (Low Subarctic)	
Mineral Terrain:	a) Open crown lichen woodland on well-drained uplands (black spruce, white spruce, paper birch; dwarf birch, ericads, <i>Cladonia</i>, <i>Stereocaulon</i>) b) Open crown conifer forest over bedrock

Table 1. continued

	c) Treeless rockland (ericads, <i>Rhizocarpon</i> , etc.)
	d) Moss forests on slope bases and lowlands (black spruce, white spruce, larch, dwarf birch, ericads, feather mosses)
Organic Terrain:	a) Peat plateaus of treed (becoming rare northward), treeless, rilled, eroding, and polygonal types (ericads, <i>Sphagnum</i> , <i>Cladonia</i>);
	b) Fens and meadows (<i>Carex</i> , <i>Eriophorum</i> , <i>Scirpus</i> , brown mosses)
	c) Bog-fens
Patterned Ground and Permafrost:	High center peat polygons; rare sorted nets and stripes in lake shallows; upland pattern typically as earth hummocks on fine-textured soils; other upland pattern rare; runnel pattern on fine-textured slopes; discontinuous permafrost in mineral soils, widespread in ombrotrophic peats
Comments:	aspen rare and typically of gnarled low stature; balsam poplar restricted to alluvium, rare and small; jack pine reaches northern limit near high boreal--low subarctic transition, rare in subarctic west of 117° W; fire return interval of 100-200 yrs; narrow marginal mats of shoreline aquatic vegetation; floating macrophytes rare; dwarf birch increases in cover to north

Forest-Tundra Region
(High Subarctic)

Note: plant communities of the some of the following vegetation types are described in section 4.6. See Plates 1-12.

Mineral Terrain:	a) Forests of single-stemmed trees or (often clonal=krüppelholz) woodlands, forest-tundras, and thickets, variable in density and spacing of trees: (1) black spruce, dwarf birch, <i>Empetrum</i> , ericads, feather mosses, lichens, <i>Ptilidium ciliare</i> (on acidic soils); (2) white spruce, dwarf birch, willow, <i>Dryas integrifolia</i> , <i>Carex</i> , legumes, <i>Rhytidium</i> , <i>Tomenthypnum</i> (on circumneutral to basic soils)
------------------	--

Table 1. continued

	b) Shrublands (dwarf birch, various <i>Salix</i> spp., and green alder) c) Medium and low shrub tundras (see section 4.6) d) Lichen tundras and rockland on bedrock; stony, or exposed ground (<i>Alectoria</i>, <i>Cetraria</i>, <i>Cladonia</i>, <i>Cornicularia</i>, <i>Lecanora</i>, <i>Lecidea</i>, <i>Parmelia</i>, <i>Rhizocarpon</i>, <i>Stereocaulon</i>, <i>Thamnolia</i>, <i>Umbilicaria</i>, etc.) e) Tussock tundras (transitional to wetland: various <i>Carex</i>, <i>Eriophorum</i>, dwarf birch, brown mosses, ericads, <i>Salix</i>, forbs)
Organic Terrain:	a) Sedge meadows (including slope fens: <i>Carex</i>, <i>Eriophorum</i>, <i>Scirpus</i>, <i>Equisetum</i>, brown mosses) b) Polygonal peat plateaus and peat polygon areas (ericads, <i>Cladonia</i>, +/- <i>Sphagnum</i>) c) Ponded, reticulate, ribbed, string, and anastomosing bog-fens, bogs, and fens (best-developed in the Hudson Bay Lowlands): dwarf birch, <i>Carex</i>, ericads, <i>Salix</i>, brown mosses, <i>Sphagnum</i>, <i>Cladonia</i>
Patterned Ground and Permafrost:	Continuous permafrost in ombrotrophic peats, widespread to continuous permafrost on uplands; high center peat polygons common; sorted nets and stripes in lake shallows common; upland patterned ground common; runnels on fine-textured slopes; stripes present; beaded streams; low center peat polygons rare; low center upland polygons rare to absent
Comments:	Important trees: black spruce dominant eastward from 114°W; white spruce dominant westward from 114°W; larch reaches highest relative cover in Keewatin; paper birch common associate of black spruce on dry to mesic acidic uplands near the southern limit of the forest-tundra, especially after fire; paper birch groves extend northward along protected brooks of the Shield; Important ericads: <i>Arctostaphylos alpina</i> (acidic soils), <i>A. rubra</i> (circumneutral), <i>Cassiope tetragona</i> (moist tundra, primarily

Table 1, continued

to north), *Ledum groenlandicum* (south), *L. decumbens* (north), *Vaccinium uliginosum* (nearly ubiquitous), *V. vitis-idaea* (usually acidic)

Fires are rare (return interval of >200 yrs); burns extend nearly to limit of trees in northwest; black spruce and larch may reach ages >300 yrs, and white spruce may reach ages >500 yrs; but normally, oldest trees in stands are 150-250 yrs; below-ground parts may reach greater ages; little shoreline aquatic vegetation

Shrub Tundra Region
(Low Arctic)

Note:

Low arctic vegetation types are similar to those in the high subarctic. The salient differences are (a) decrease in community stature, biomass, and productivity; (b) decrease in importance of dwarf birch, *Salix glauca*, and ericads; (c) increase in importance of *Dryas*, *Cassiope*, lichens and mosses; (d) peat polygon areas and low center polygons replace peat plateaus; eroding peats become less common northward. For important plant communities and associations of the low arctic, see section 4.6.

Patterned Ground and Permafrost:

Continuous permafrost, except in minerotrophic peats and under lakes (although permafrost extends under lakeshores); high and low center peat polygons; upland patterned ground widespread; runnels and stripes common; sorted nets and stripes in lake shallows widespread where boulders present; solifluction and gelifluction on slopes; beaded streams

Comments:

Little or no shoreline aquatic vegetation; fires rare, except in northwest

4.2 Patterned ground in relation to vegetation and terrain in the study region

Figures 4-7 depict the occurrence of peatland polygons, runnels and stripes on slopes, upland patterned ground, and patterned ground in lake shallows. The bold black line in each figure delimits the study region. These distribution maps provide information on terrain and parent materials, and indirectly, on climate. No attempt was made to differentiate between active and relict features.

4.2.1 Peatland polygons

Peatland polygons are the most widespread of the selected patterned ground features, extending south of the study region as high center polygons in peat plateaus and palsas. In the forest-tundra, polygonal peat plateau--bog-fen mixed wetlands are common. Near the northern limit of trees, peat plateaus pass into smaller, darker-toned peat polygon areas. As common and conspicuous forms, low center polygons are restricted to the low arctic and northward.

Peatland polygons show the most widespread occurrence of the patterned ground types reported here, as they extend southward beyond the study region (Figure 4). These polygons are predominantly of the high center type, but by the low arctic, low center polygons become locally conspicuous, marking a transition

from inactive to active ice wedges (Brown 1973). While peatland polygons extend well to the north of the forest-tundra, they are usually limited in areal cover as the ombrotrophic peats in which they occur become restricted in area. Minerotrophic sedge peats (=embryonic mires) are the dominant peat landform in the arctic, and these wet peats are less prone to formation of conspicuous polygons.

Treeless peat plateaus are the predominant landform exhibiting high center polygons in the study region. These often extensive peat landforms reach their greatest abundance in the low subarctic and extend north into the southern portion of the forest-tundra. Peat plateaus are often spatially connected to bog-fens and fens in successional-related mixed wetlands (cf. Zoltai 1973; Hardy 1976; Dredge and Nixon 1979; field observ.).

Bog-fen complexes can be found in any proportion of bog to fen within the subarctic. In the continuous permafrost zone (high subarctic and northward), bog types (commonly peat plateaus, palsas, and peat mounds) show evidence of encroaching on fens, whereas in the widespread and discontinuous permafrost zones (high boreal to high subarctic), fens are commonly encroaching on degrading peat plateaus and palsas (Bradley et al. 1982; Mollard 1982).

Northward from within the forest-tundra, peat plateaus pass into smaller, darker-toned peat polygon areas (Zoltai, pers. comm.; field observ.); and southward through the low subarctic, peat plateaus become treed and lose polygonal pattern (cf. the 'bog treeline' of Bradley et al. 1982). Thus, although nearly

ubiquitous, high center peat polygons reach their greatest prominence in a band encompassing the northern portion of the low subarctic and the southern portion of the forest-tundra.

Between Great Bear and Great Slave Lakes, bedrock control expresses itself in decreasing the occurrence of peatland polygons. Peatlands of the high boreal and low subarctic there are usually restricted to bedrock depressions. As such, they tend to be small in area and often treed. Polygons, if present, are difficult to discern.

In the extreme northwest, conspicuous peatland polygons are sparse in the upper and middle Mackenzie Delta. Although they are inconspicuous in the upper Delta on small-scale airphotos, Mackay (1974: Figure 28) reports them to be numerous. In the lower Delta, they are common as both high and low center polygons. Low center polygons are extremely abundant in the flats of Tuktoyaktuk Peninsula (Mackay 1974) and elsewhere on the Arctic Coastal Plain. In the extreme southeast, peatland polygons are by far the predominant form of patterned ground in the Hudson Bay Lowlands.

Low center polygons are arctic in distribution and indicative of active ice wedges (Brown 1973). They are usually associated with poorly-drained, peat-covered silts in depressions (Mollard 1982). Within the study region they reach their greatest prominence on the Arctic Coastal Plain of the northwest, often as orthogonal polygons in drained thaw lakes. Inland from the Arctic Coastal Plain, low center polygons are much less conspicuous and evidently less common. This is especially true on the low arctic

Shield in the Mackenzie District where broad poorly-drained depressions are scarce (airphoto data).

4.2.2 Runnels and stripes

In the northwest, elongate slope pattern extends southward from the low arctic through the low subarctic. The predominance of runnels in the northwest indicates seasonally saturated, ice-rich slopes composed of fine-textured soils. The sharp drop in occurrence of linear slope forms at the Shield is notable. Across the Mackenzie District, conspicuous runnels and stripes are uncommon to rare. Locally in Keewatin and along the lower Thelon River, elongate pattern and slopewash are common.

Elongate slope features form a continuum from straight sorted stone stripes, through non-sorted semi-sinuuous and sinuous forms that may act as spring runoff channels. For example, west of the Dismal Lakes, linear patterns occur on slopes which may be both runnels and stripes. Indeed some stripes may be initiated by runneling (rillwork), and most sorted stripes normally carry drainage (Washburn 1980). Crampton (1974) has described linear-patterned slopes in the central Mackenzie valley on which sub-parallel peaty ridges (evidently formed by frost action) alternate with runnels, resulting in two types of linear slope features. The peaty ridges were thought to be "partly fossil". As it is not always possible to separate these forms, their

combined occurrence is depicted (Figure 5). Two kinds of information may be gleaned from Figure 5: texture of parent material and presence of permafrost.

High cover of elongate slope forms (as runnels) in the northwest is evident. North from the Great Bear River and westward to the Mackenzie River, runnels are the most conspicuous form of patterned ground. In the Mackenzie Delta, however, runnels are absent due to insufficient slope. In the Cordillera, both stripes and runnels are present.

Runnels occur as the dominant form eastward from the Mackenzie Delta to about the Horton River where runnels, stripes, and intermediate forms all occur. From the Horton to the Coppermine Rivers intermediate forms appear the most conspicuous, at least from the air. In the valley of the Coppermine, runnels and less well-defined slopewash abound.

The sharp drop in occurrence at the Shield is notable. As runnels require fine-textured soils for their formation, this drop in occurrence is likely more indicative of a change from fine- to coarse-textured soils, rather than a warmer climate. The slower drainage and shallower active layers of fine-textured soils favor surface flow of meltwater. The sandy soils of the Shield, with their more rapid drainage and deeper active layers, favor subsurface flow of water and, hence, are usually not conducive to runnel formation. Furthermore, slopes on the Shield tend to be short, and thus not conducive to formation of obvious linear features.

Across the subarctic Shield, conspicuous runnels and stripes

are uncommon to rare. Their occurrence increases by the low arctic, and where they occur they may be indistinguishable as to runnel or stripe, or are transitional to elongate nets. In the Mackenzie District, elongate slope forms are conspicuous only in the low arctic and rare in the northern part of the forest-tundra, making them a good indicator of the high subarctic--low arctic transition.

The minor cluster along the lower Thelon indicates runnels (and slopewash). In Keewatin, elongate slope forms are not unusual, and appear to be most prevalent in areas of glaciolacustrine or glaciomarine inundation. It is also possible that longer more gentle slopes are present which might favor formation of conspicuous patterns.

The vegetation of runnels varies across the subarctic and low arctic but is always moister than that between runnels. In the cordillera of northern Yukon, Wiken et al. (1981) recorded willows and "aquatic sedges" in the runnels and tussock tundra between runnels.

In the subarctic northwest, spruce, shrubs, and *Sphagnum* in the runnels contrast sharply with the white, lichen-covered (primarily *Cladonia*) interfluves. This dark/white runnel/interfluve pattern is obliterated by fire, such that burned areas are invariably dark-toned on airphotos. A dense stand of trees and/or shrubs usually indicates a fire in the recent past; peat accumulation and permafrost aggradation associated with post-fire recovery in these stands bring about self-thinning (Black 1977). The less dense stands, with well-developed runnel

pattern, are the more mature (Zoltai, pers. comm.).

In the high subarctic and low arctic of the Shield, wet runnel vegetation is often light-toned and dominated by *Carex-Eriophorum-Equisetum* slope fens or meadows within an upland tundra matrix (this study). In the middle Coppermine--Dismal Lakes region, darker-toned runnels and/or stripes are often dominated by low shrubs of dwarf birch, *Ledum decumbens*, *Salix*, and *Cassiope tetragona* in a *Dryas* upland tundra matrix (this study).

On the Shield in Keewatin, an upland tussock tundra of *Eriophorum vaginatum-Ledum decumbens/Sphagnum* may cover runnels (Hardy 1976). Through peat and ground ice accumulation the organic surface may dry out leading to decline of *Eriophorum* and mosses; older senescent portions may become dominated by *Ledum decumbens*, *Vaccinium vitis-idaea*, and other shrubs with lichens and feather mosses (Hardy 1976). These shrub/moss communities are usually darker-toned than the surrounding low shrub/lichen tundra.

4.2.3 Upland patterned ground

The southern limit of conspicuous upland patterned ground coincides fairly closely with the southern limit of the forest-tundra. An exception lies in the northwest where earth hummocks extend south through the low subarctic on loamy soils. On the Shield, circles (including mudboils) and nets predominate.

Trees are generally absent from polygonally patterned uplands, due, most likely, to droughty conditions on sandy soils.

The occurrence of upland patterned ground, here including the continuum of forms from polygons to nets (including earth hummocks) and circles (including mudboils) is depicted in Figure 6. The southern limit of conspicuous upland patterned ground provides a good indicator of the southern limit of the forest-tundra. The major exception lies in the northwest, principally west of the Anderson River. Here, earth hummocks extend south through the low subarctic on heave-prone silty clay loams and loams. On airphotos, these earth hummocks appear as a faint mesh in forest communities, as though a fine cheese cloth were imbedded in the surface of the photographic paper.

Southeast from Great Bear Lake the correlation of upland pattern and contiguous forest-tundra limits is better than in the northwest, and may correspond to a transition to coarser-textured loamy sands and sandy loams typical of the Shield. Patterned ground also occurs in the forest-tundra highlands of the Cordillera, the Franklin Mtns, Grizzly Bear Mtn, Scented Grass Hills, and Colville Hills.

Dense vegetation tends to conceal patterned ground, so that its distributional limit as determined by airphotos probably lies north of that determined by fieldwork. Thus the close correspondence of forest-tundra and patterned ground may be spurious in that low subarctic pattern is difficult to detect. The true southern limit of patterned ground may lie southward of that

depicted in Figure 6. Conversely, some of this pattern may be relict, and thus the southern limit of climatically relevant upland pattern might lie farther north. The apparent close correlation of the forest-tundra/upland pattern limits is nevertheless intriguing and requires further research.

Geographic variations exist in the relative abundance of these equiforms. Earth hummocks (non-sorted mounds) dominate in the fine-textured soils of the northwest along with runnels. With the exception of earth hummocks and runnels, conspicuous patterned ground would be rare in the northwest. On the Shield, mudboils (sorted circles) and mounds predominate; where abundant, they lend a freckled appearance to Shield upland tundra as viewed on airphotos (Plate 1). Some drumlin crests and tills show polygonal pattern, but polygons are typical only on coarse-textured, often water-sorted deposits (see Shilts 1974 for patterned ground and terrain type relationships). These polygons are overwhelmingly of the high center type; low center polygons were observed only at the northern limit of the forest-tundra and adjacent low arctic.

Just as features such as beaded streams, pingos, peat plateaus, and palsas are indicative of permafrost (Zoltai 1971; Brown 1973; Mollard 1982), patterned ground can be indicative of terrain types. Prevalent forms of patterned ground in the forest-tundra are considered below with reference to terrain interpretation.

Mudboils are round to elongate bare soil patches that form on perennially-frozen shock sensitive poorly-sorted tills, marine silty clays, and fine-textured colluvium with appreciable silt and/or clay content (Shilts 1978; Zoltai and Woo 1978). Low

liquid limits (8-20%) and plasticity indices (0-10%) are characteristic of Shield tills (Scott 1976), such that at low moisture contents Shield tills pass almost directly from a semi-solid to a liquid state (Zoltai and Johnson 1978). These properties favor the formation of mudboils over pattern dependent on frost-cracking (Shilts 1974). Diapiric injection of mud driven by pressures resulting from excess pore-water supplied by rain, thawing ground ice, or mechanical disturbance has been identified as the formative process for mudboils (Shilts 1978).

Mudboils are conspicuous in well- to imperfectly-drained upland tundras and forest tundras of the Shield where soil moisture contents are at or near liquid limits. They typically occupy convex surfaces or gentle slopes and merge in form with nets (Plate 1), or with steps and stripes on steeper slopes. As active features they evidently do not extend south of the forest-tundra ("treeline" of Shilts 1978), and much of this pattern in the forest-tundra is probably inactive as indicated by vegetation-covered centers (field observ.).

A related feature, earth hummocks (mud hummocks, non-sorted nets, non-sorted circles of various authors) form on perennially frozen loamy soils (Zoltai and Pettapiece 1973, 1974). In the northwest, they extend southward from the low arctic through the low subarctic in imperfectly-drained (most common) to well-drained tundra, forest-tundra, and forest. They occur on the silt loams of the Coppermine--Dismal Lakes region (field observ.). Earth hummocks are more common in the northwest than in Keewatin (Tarnocai and Zoltai 1978).

Diapirs or ice wedges are absent in earth hummocks and the formative process is intermittent frost-heave above the permafrost table (Tarnocai and Zoltai 1978). There is no indication of liquifaction or shock sensitivity, and the high plasticity of the fine-grained soil prevents the mound from flattening out, resulting in a generally hemispheric cross-section (Zoltai and Tarnocai 1981). Quasi-stability may be achieved when hummocks have reached sufficient size for their upper portions to become relatively well-drained (Zoltai and Pettapiece 1974). Southward through the low subarctic, leaning trees are fewer, indicating greater soil stability (Zoltai and Pettapiece 1974).

Textures of these hummocky soils are silty clay loam, silt loam, and loam (Zoltai and Pettapiece 1974; field data). These soils are heave-prone since soil particles are sufficiently small to be ejected by ice crystals, and hydraulic conductivity is high enough to rapidly supply water to the growing ice (Anderson et al. 1984).

Frost cracks, typically in a polygonal pattern, are found on coarser-textured, often water-sorted sands with high liquid limits and an insignificant fine-grained component (Shilts 1974). They are characteristic of outwash plains, eskers, ribbed moraine, beaches, deltas, and alluvium. In depressions, polygonally patterned soils typically have a thick organic layer and/or a low pH (Shilts 1974). These polygonal forms require soil stability to allow seasonal growth of ice wedges; the unstable soil conditions required for mudboil formation would destroy frost cracks and thus these features are rarely encountered together (Shilts 1974).

Conspicuous polygons are found in permafrost terrains from the arctic southward through the high subarctic, typically in tundra communities, rarely forest-tundra or forest. Trees are generally absent from polygonally patterned landforms due, most likely, to dry soil conditions on coarse-textured soils and to thick organic mats in depressions. In the forest-tundra and low arctic many upland polygons may be relict or inactive (Bradley et al. 1982; field observ.). Active ice wedges in North America are apparently confined to the continuous permafrost zone (Brown 1973), which includes the forest-tundra of the northwest, and the northern portion of the forest-tundra eastward from Great Bear Lake. The apparent rarity of active ice wedges in upland polygons in the forest-tundra is surprising in that mean annual temperatures (-6.5 to -10.5 C) are likely sufficient for growth of ice wedges (Brown 1973; Washburn 1980; i.a.).

4.2.4 Sorted patterned ground in lake shallows

Conspicuous patterned ground in lake shallows is rare in the northwest due most likely to the scarcity of boulders and cobble in the parent materials and to the low cover of lakes. On the Shield, the southern limit of lake shallow pattern correlates well with the southern limit of the forest-tundra, extending somewhat farther south than upland pattern.

The occurrence of sorted patterned ground in lake shallows, including sorted stripes (rib and trough pattern of Shilts and Dean 1975), sorted nets (sorted or stone circles of Dionne 1974; Mackay 1967; and Walters 1983), sorted polygons (Ray et al. 1983), subaqueous mud boils (Shilts 1974), stone pits, and intermediate forms (such as amoeba-shaped polygons of Dionne 1974), is depicted in Figure 7. In all forms, fines occupy the prominences and cobbles and/or boulders the depressions.

Conspicuous patterned ground in lake shallows is rare in the northwest for two reasons: lakes are scarce and boulders and cobble occur only locally. West of the Anderson River, they verge on absence from the landscape. Features smaller than 2-3 m in diameter occur, such as small sorted stone circles reported by Mackay (1967) on Garry Island, but many of the smaller forms would not be discernible on 1:50,000 scale airphotos. The occurrence of upland patterned ground in the northwest (Figure 6) would likely resemble that of patterned ground in lake shallows (Figure 7) were it not for earth hummocks.

Elsewhere, the southern limit of patterned ground in lake shallows correlates well with the southern limit of the forest-tundra. Lake shallow patterned ground extends somewhat farther south than upland patterned ground, as it is sporadic in the low subarctic. I observed it on the ground in the low subarctic region along the Snare, Yellowknife, McCrea, and Beaulieu Rivers. Zoltai (pers. comm.) has observed lake shallow pattern in the subarctic of Keewatin and adjacent Manitoba. As an extreme rarity, lake pattern may be observed in the high

boreal region; e.g., along the shore of McVicar Arm, and NW of Hottah Lake (airphoto observ.).

In general, lake shallow pattern extends farther south than the apparent southern limit of upland patterned ground. This may be due both to the concealing effects of upland vegetation and perhaps to less constraining conditions on the formation of underwater patterned ground (see Ray et al. 1983).

Modes of formation of sub-aqueous patterned ground remain the topic of debate. Some argue that sub-aerial conditions followed by inundation seem to be required (Dionne 1974; Walters 1983), while others present evidence indicating underwater formation (Mackay 1967; Shilts and Dean 1975; Washburn 1980). Shilts (1978) considered sub-aqueous rib and trough patterns to be genetically related to mudboils. Ray et al. (1983) noted that most large active sorted polygons in the Southern Rockies are on the beds of ephemeral ponds.

Patterned ground in lake shallows (Plate 2) occurs commonly in the subarctic and abundantly in the low arctic of the NWT down to water depths of 1.5-2 m (Shilts and Dean 1975; field observ.). Their widespread occurrence (Figure 7) in permanent lakes argues against a requirement for sub-aerial formation. It is possible, however, that much of this underwater patterned ground is relict, dating from previously lower water levels. But this seems unlikely for two reasons. Wave forces and plucking of cobble and boulders by down-freezing lake ice, coupled with chaotic movements of ice during spring break-up, would act to disorganize the fines in pattern centers and the coarse clasts in the troughs. Such

sharp boundaries between clasts likely requires some active maintenance process. Secondly, lake shallow pattern occupies a definite zone from lake edge to a depth which may correspond to the lower limit of freezing of winter lake ice to lake bottom (Shilts and Dean 1975). Were these features relict and dependent on sub-aerial formation, they would show a less regular lower limit related to the idiosyncrasies of former water levels.

With the exception of the northwest, where fine-textured parent materials predominate and lakes are few, the southern limit of lake shallow pattern corresponds well with the southern limit of the forest-tundra. Across much of the study region this corresponds to a mean annual air isotherm of -7 to -8 C (-3.5 to -4.5 C soil isotherm). Dionne (in low subarctic Quebec; 1974) and Walters (in low subarctic Alaska; 1983) described patterned ground in lake shallows where the current mean annual air temperature is -4 C. In both studies the authors concluded that the patterns were probably formed sub-aerially during low water periods. Dionne (1974) concluded that the features were formed in the recent past, possibly within the last two centuries, and are probably younger than 1-2 thousand years.

The formation and status of the extensive lake shallow patterned ground in the high subarctic and low arctic require further study. In any case, the southern limit of these often striking features remains an excellent abiotic indicator of the southern limit of the forest-tundra transition across most of the NWT.

4.3 Landscape cover of the study region

4.3.1 Water bodies

Cover of water bodies varies across the study region, reaching a minimum in the northwest; across the Shield water cover ranges from 10-25%; highest water cover is reached on the Arctic Coastal Plain, the Hudson Bay Lowlands, and at the interface of the Paleozoic basin and the Shield.

Eight water regions are apparent (Figure 8A). In the Mackenzie Delta, water cover increases from about 10% in the south to >50% in the north. Here innumerable shallow ponds and small lakes, of flooding and thermokarst origin, dot the landscape. On nearby Richards Island and Tuktoyaktuk Peninsula, water cover is generally >25%.

In that small portion of the Cordillera sampled, water cover is slightly >0%, and never exceeds 2%.

Across most of the northwest, water occupies 2-10% of the landscape. Lakes are small and often round or regular in outline. Locally, water cover falls below 2%, such as in the Melville Hills and near the upper Horton. The major exception lying within the Paleozoic basin is the Colville Lakes where five moderately large lakes result in an average water cover of 10-25%. In the middle Anderson region, lakes are small but numerous, bringing the cover for water above 10%.

Great Bear and Great Slave Lakes straddle the Paleozoic basin and the western rim of the Shield. Other large lakes also occupy the trough lying west of the Shield, e.g., Hottah and Faber Lakes.

Along the raised western rim of the Shield, rockland dominates, lakes are small and occupy about 5-15% of the landscape.

Across most of the Shield, water occupies 10-25% of the landscape. Lakes are numerous and vary greatly in size.

Lakes cover only 2-10% across a large inlier of Proterozoic sediments, principally sandstones, of the Thelon Plain.

In the Hudson Bay Lowlands, water cover exceeds 10%. Extensive ponded organic terrain may bring water cover above 25%. The large peak along the coast results from extensive ponding and from inclusion of marine waters in coastal photos.

4.3.2 Rockland

Rockland reaches peak cover along the raised western rim of the Shield and elsewhere north of Great Slave Lake (10-35%). In comparison, the Shield east of Great Slave Lake is rather gentle (rockland $\leq$ 5%). With the exception of the Cordillera and the vicinity of the Melville Hills, the northwest is virtually free of rockland.

Some fairly well-defined peaks in rockland appear, as shown in Figure 9A. In the Cordillera, as much as 10% of the terrain, due

to bold summits and steep slopes, is classed as rockland. About 5% of the Norman Range (Franklin Mountains) is rockland. To the north of Great Bear Lake, areas of dolomite and limestone bedrock have little surficial cover such that up to 15% may be rockland.

The western rim of the Shield, bordering on the Paleozoic basin, is a region of relatively bold bedrock summits. These crystalline rock ridges bear little soil and offer restricted growing conditions to zonal vegetation. In general, 10-35% of the terrain may be classed as rockland, with some areas exceeding 50% rockland (e.g., NE of Port Radium).

Most of the large contiguous areas of Shield rockland are found north of Great Slave Lake. Remarkably rocky terrain (up to 60% rockland) is found NNE of Takiyuak Lake on acidic crystalline rocks and related metamorphics. South-southeast from Takiyuak Lake, past eastern Point Lake, and south to Courageous Lake, rockland occupies 10-25% of the landscape (Plate 3).

Around the East Arm of Great Slave Lake and in the vicinity of Healey Lake, rockland occupies 10-25% of the landscape.

East of the Thelon, and west of Dubawnt Lake, the sedimentary terrain is gentle, with little or no rockland. Locally, across the Shield from Great Slave Lake east to Hudson Bay, areas with >10% rockland exist (e.g., between Whitefish and Campbell Lakes), but most of the eastern Shield is rather gentle; rockland rarely occupies >5% of the terrain.

4.3.3 Shrubland

Dwarf birch, willow, and alder shrublands occupy 2-10% of the landscape in the study region. Peak cover is reached in the middle third of the Mackenzie Delta, in portions of the Hudson Bay Lowlands, and locally elsewhere. In most cases, tall shrub cover >10% is due in part to burn or rockland influences.

Shrubland shows a general decline in cover from south to north. There is a semblance of a "shrubline" lying north of the limit of trees. Beyond treeline, tall shrubs are clearly restricted to protected well-watered sites.

Peak shrubland cover (>50%) is reached in the central third of the Mackenzie Delta. North of this tall shrub zone, wetland dominates, and to the south, trees dominate.

Elsewhere across the forest-tundra, shrubland cover ranges from 2-10%. In general, any cover value for shrubland exceeding 10%, outside of the Mackenzie Delta and portions of the coast of Hudson Bay, is probably due at least in part to burn or rockland.

Waist-high dwarf birch and *Salix* (primarily *S. glauca*, *S. arbusculoides*) form an often extensive matrix in spruce woodland on well-watered slopes in the subarctic. Typically, these communities were classed as treed. Seldom do extensive dwarf birch and willow occur without trees, with the common exception of burn-induced shrub.

Dwarf birch, willow, and alder in the high subarctic of the

Shield occupy slope bases, shores, drainages, and wetland margins. Commonly birch and willow shrubs occupy the troughs of elongate nets on patterned slopes. Though often not exceeding 1 m in height, these dense birch-willow communities contrast sharply with the typical lighter-toned upland tundras, and were classed under shrubland.

Three anomalous peaks for shrubland are evident. East of the Anderson River (at about 127°30'W, and 69°N), >35% of the terrain is heavily stippled on airphotos. This appears to be alder (and dwarf birch?) with or without willow.

At Camsell Lake, south of Mackay Lake, >30% of the thin-till terrain is covered with a dark-toned vegetation with patches of black spruce. The area resembles a burn, but its northern location and the treelessness of islands and many peninsulas argue against a forest pre-dating a fire.

Shrubland reaches a maximum cover of about 25% in the hummocky ground moraine of the summits of Grizzly Bear Mountain. This cover value includes only "pure" shrubland; tall shrubs are also extensive as an understory for trees there.

4.3.4 Wetland

Wetland reaches maximum cover in the Mackenzie Delta and the Hudson Bay Lowlands (>85%). Along the Arctic Coastal Plain, wetland cover commonly exceeds 25-50%. High cover is also reached west of Great Bear Lake, in SE Mackenzie District, and in eastern

Keewatin. Elsewhere, wetland covers 2-10% of the landscape.

Peak wetland cover is found in the extensive lowlands at the western and eastern extremes of the study region (Figures 11A, B). Wetland cover in the Mackenzie Delta peaks at nearly 100% at the seaward edge of the delta. Eastward, wetland values drop rapidly at Richards Island. The western end of Tuktoyaktuk Peninsula supports about 25% wetland, with values increasing to >50% to the east.

Along the Arctic Coastal Plain eastward to Horton River, wetland exceeds 25%, and 50% at the mouth of the Anderson. The southern end of Parry Peninsula is crossed by a band of heavily ponded wetland peaking at about 35% cover.

The study region again reaches the arctic coast at the Coppermine River where wetland cover exceeds 50%.

Inland, treeless peat plateaus attain high cover north of Lac Maunoir at 33%, and in the Mahony Lake area west of Great Bear Lake, where treeless bogs are extensive. Wetland covers >25% in a small area east of Byland Bay on the south shore of Smith Arm, Great Bear Lake.

Eastward, wetland covers 2-10% across the eastern Mackenzie District. Peat plateaus to the south and bog-fens and tussock wetlands to the north reach cover values of 25-50% in the vicinity of the upper stretches of the Thelon, Dubawnt, and Kazan Rivers. The extensive white-toned (*Cladonia* covered) peat plateaus are especially striking between Wholdaia, Snowbird, and Kasba Lakes in the SE Mackenzie District.

Across Keewatin, wetland cover is generally higher than on the Shield to the west. Western and central Keewatin wetlands (bog-fens, various fen types, peat polygon areas) cover 5-25% of the terrain. Wetland covers 25-50% in an area NNE of Ennadai Lake.

In eastern Keewatin, wetland covers >25% of the terrain, exceeding 50% at the Hudson Bay coast. In northern Manitoba, wetland cover increases from west (2-10%) to east. Farther east, the Hudson Bay Lowlands are reached, and wetland dominates the terrain, reaching values >85% between the North Knife and Churchill Rivers.

Wetlands of the Hudson Bay Lowlands occur in areally complex forms that are evidently in a state of dynamic flux between relatively high and dry bog forms and lower, wetter bogs, fens, and bog-fens. Salt marshes occupy a band along the coast.

4.3.5 Wetland plus shrubland.

Wetland--shrubland occupies 5-25% of the landscape in most of the study region, thereby restricting maximum cover of zonal tree and tundra vegetation to 75-95% dominance of the landscape.

As most tall shrub vegetation requires abundant water, this composite of wetland plus shrubland displays the cover of lowland or "wetland" in a broader sense (Figures 12A, B). Generalizations made for shrubland and wetland apply here. In addition, a number

of other points are evident.

The middle and lower stretches of the Mackenzie Delta are dominated by this "wetland" vegetation. Tuktoyaktuk Peninsula again increases in "wetland" cover from west to east, with >85% reached by 131° W.

A band of wetland--shrubland cover >10% is evident along the upper Snare River. This cover is composed of dwarf birch--blue green willow shrub, bog-fens, and peat plateaus.

In the middle section of the Thelon valley, SW of the Ursus Islands, wetland--shrubland reaches a cover >25%.

In the Hudson Bay Lowlands, this type reaches greater dominance, and does so farther west, than does wetland alone.

Between the extremes of the Mackenzie Delta and the Hudson Bay Lowlands, wetland--shrubland generally occupies 5-25% of the landscape. The occurrence of wetland--shrubland is primarily a function of drainage conditions, hence these treeless lowlands restrict the maximum cover of zonal vegetation (forest and tundra) to values of 75-95% dominance of the landscape.

4.3.6 Upland tundra

Upland tundra cover gradients typically show a steep rise near the southern limit of the forest-tundra in the southeast, and near the northern limit in the northwest. The 0-85% gradient spans as little as 15-25 km in areas of steep topoclimatic change, but more typically spans 45-135 km; in the southeast, the gradient is most

gradual, spanning 200-330 km. Southern outliers of upland tundra in the northwest are correlated with highlands such as the Colville Hills and Scented Grass Hills.

Burned upland tundra (rare to occasional, observed on airphotos only in the northwest) was recorded under upland tundra. Although tundra burns are not uncommon in the northwest and perhaps elsewhere (Wein 1975), their detection on airphotos is difficult after only a few years of recovery (Cochrane and Rowe 1969; Wein and Bliss 1973).

Cover of upland tundra ranges from 0 to >90% for the study region (Figures 13A, B; Plates 4-6). Eastward from north of Great Slave Lake, upland tundra rises abruptly to high values near the southern limit of the forest-tundra. Westward from the Horton River, upland tundra rarely attains 85% cover due to the combined effects of trees, wetlands, and shrublands. Indeed, upland tundra is virtually absent in the Mackenzie Delta proper-- due simply to the scarcity of uplands.

The steepness of the N--S gradient of change of upland tundra cover varies greatly. On the east slope of the Cordillera, and from the Mackenzie River to the Caribou Hills, the 0-85% change can take place within 20-25 km due to the steep topoclimatic gradient. Between the Mackenzie and Anderson Rivers, the gradient of change from 0-50% cover is quite variable. Along the longitude of the Kugaluk River, e.g., 0-50% is achieved in about 125 km, whereas along the Anderson, the same vegetation change takes only 15-20 km. The southern limit of upland tundra is irregular in the

Anderson--Colville Lakes region; this point is discussed below.

Northeast from the middle Anderson, the vegetation change is generally abrupt. The 0-85% gradient takes place over 35-85 km.

North from Dease Arm of Great Bear Lake, the vegetation change is amazingly rapid; upland tundra may increase from 25-85% cover in 10-15 km. Northward from midway between Smith and Dease Arms of Great Bear Lake, upland tundra increases swiftly to >50% cover due to the steep topoclimatic gradient of the Big Spruce Hills.

Eastward from Great Bear Lake to Winter Lake, there are large variations in both gradient and orientation of the upland tundra contours. Although the 0% contour assumes a NNW--SSE orientation, other contours change directions repeatedly in a complex response to synoptic climate, local topoclimate, and changes in parent material.

On Takaatcho Peninsula, between Dease and McTavish Arms of Great Bear Lake, contour lines of percent cover roughly parallel the outline of the lake. The center of Takaatcho Peninsula rises over 300 m above the level of Great Bear Lake. Northeastward, at the base of the peninsula, the land has risen another 150 m, and cover of upland tundra apparently reflects this topoclimatic gradient. Farther east, near Lady Nye Lake, some uplands exceed 700-730 m, over 550 m above the level of Great Bear Lake; this is reflected in the southward dip of the 85% contour.

Although the southern limit of upland tundra drops SSE from McTavish Arm, upland tundra remains low in cover until east of the Coppermine River. Eastward from the Coppermine River north of Rocknest Lake, upland tundra rises in cover from 10-85% in as

little as 25-30 km. Nearby, about 15 km north of Rawalpindi Lake, upland tundra occupies 85% of the terrain. To the north, upland tundra decreases in cover to <10%, replaced in large part by tree vegetation. Not until 175 km north of Rawalpindi Lake does upland tundra again reach 85% cover.

Conversely, proceeding SSE from north of Rawalpindi Lake, upland tundra remains above 85% for another 80 km. Thence south, from the upper reaches of the Indin River, upland tundra cover drops rapidly to zero on a line through Indin Lake and the south shore of Snare Lake. Here the 0-85% gradient may be as abrupt as 35 km.

Clearly then, in the region between 114° and 117°W, a N-S gradient in upland tundra cover hardly exists. From the southern limit of upland tundra near Indin Lake, 320 km must be traversed to the north shore of the eastern Dismal Lakes before upland tundra gains complete dominance over tree vegetation.

Southeastward from the Snare River, to the East Arm of Great Slave Lake, upland tundra contours swing to a SE orientation. The 0-85% gradient spans 45-135 km. North of the East Arm of Great Slave Lake, vegetation change is rapid; the 0-85% gradient spans 20-70 km, with an average width of 40 km.

Eastward from Great Slave Lake to near Coventry Lake, the 0-85% gradient ranges between 45-110 km; the steepest gradient is found NE of Porter Lake.

From Coventry and Rennie Lakes, eastward to the coast of Hudson Bay, a number of factors likely combine to make the 0-85% gradient the most gradual of the entire forest-tundra. Indeed, northward

from the Wholdaia--Kasba Lakes region, some 200-330 km must be traversed before the 85% continuous contour is reached.

Across northern Manitoba and southern Keewatin, the corresponding 0-85% gradient spans 210-330 km. Local decreases in the overall northward increase of upland tundra are evident along the Manitoba--Keewatin border and elsewhere in southern Keewatin. These dips in upland tundra cover are mirrored by increases in wetland, and less so by trees and shrubland.

In contrast to the 0-85% gradient, the 0-50% gradient in northern Manitoba and southern Keewatin is only slightly more gradual than that of the Shield to the west. The 0-50% gradient ranges from 34 km NNE from Shethanei Lake on the Seal River to 100 km from 60° N near the Saskatchewan--Manitoba border NNE to Ennadai Lake.

In the Hudson Bay Lowlands, upland tundra cover does not exceed 2% and is restricted to beach ridges, and stony and sandy glaciofluvial (and till?) deposits.

The southern (more properly: low subarctic) limit of upland tundra is most irregular in the northwest. Here, major landscape discontinuities such as (a) the Cordillera; (b) outliers of the Cordillera such as the Norman Range; (c) isolated uplands such as the Colville Hills, highlands west of Keith Arm, Scented Grass Hills, and Grizzly Bear Mountain on Great Bear Lake; and (d) the broad poorly-drained Mackenzie Valley; exert their influence on the percent cover of upland tundra.

The rather surprising peak of upland tundra (>25%) lying north

of Lac des Bois is due to the Colville Hills. Maximum elevation here peaks at 650 m, 360 m above the lowlands.

Northwest of Aubry Lake lies an unusual peninsula of upland tundra on coarse-textured hummocky ground moraine. Here the maximum elevation is not great, lying between 305-410 m, and upland tundra reaches 5% cover likely due to the influence of dry soils. A more detailed account of the southern limit of upland tundra is found under section 4.3.17.

In general, upland tundra cover increases rapidly northward somewhere across the forest-tundra. This rapid change occurs typically at the southern limit of the forest-tundra in the southeast (Figure 13). In the northwest, the rapid change in upland tundra cover often takes place at the northern edge of the forest-tundra. Westward from Hudson Bay to about the Snare River north of Yellowknife, upland tundra shows an abrupt southern limit. In contrast, compare the areas east of Great Bear Lake, east of the Colville Lakes, or west of the Anderson River. In those places, the steep rise in upland tundra cover tends to lie at the northern limit of the forest-tundra, mirrored by correspondingly opposite changes in tree cover. This topic is described in more detail under section 4.3.17.

Figures 13A.1 and A.2 detail percent cover of upland tundra from a 3-dimensional perspective, and differ only in the viewer's orientation. The southward decrease of upland tundra shows the characteristic steep gradient. The roughness of the surface indicates the natural variation in the vegetation. These bumps

and depressions may be minimized by increased averaging. The resulting smoothed plots lose local accuracy, but are comparable with synoptic climatic maps. Smoothed upland tundra cover (Figure 14) is described along with smoothed tree cover under section 4.3.18.

4.3.7 Upland tundra plus rockland

Comparison of Figure 13B (upland tundra) with Figure 15B (upland tundra plus rockland) reveals the contribution of rockland to total cover of treeless uplands. Treeless uplands never reach zero cover between Great Bear and Great Slave Lakes along the western rim of the Shield, where 10-25% of the landscape may be treeless southward beyond the forest-tundra. East of Great Slave Lake, contours of percent cover of treeless uplands lie only slightly farther south of those of upland tundra.

Rockland may be confused with climatically sanctioned upland tundra, e.g., east of McTavish Arm of Great Bear Lake, and NE of the East Arm of Great Slave Lake, where both upland tundra and rockland exist. Elsewhere, rockland and fire are clearly the only sources of treeless uplands. Glacially scoured bedrock, or excessively stony terrain, usually supports treeless communities, regardless of the climate. In the high subarctic, rockland only rarely supports low spruce. Southward in the low subarctic and high boreal, jack pine and black spruce are the dominant trees of

bedrock terrain, but are normally restricted to bedrock fissures and depressions where soil and organic matter accumulate.

Scoured acidic bedrock commonly supports lichen and low shrub communities. Crustose lichens such as *Rhizocarpon*, *Lecidea*, and *Umbilicaria* are dominant on the scoured convexities. Low ericads, *Cladonia*, *Stereocaulon*, and *Dicranum* species (with *Cornicularia* and *Alectoria* northward) are prominent in the cracks. Deeper depressions may support boggy communities of ericads, *Sphagnum*, and *Cladonia*. Where trees exist, the landscape presents a mosaic of edaphic lichen, shrub, and tree communities.

Excessively stony acidic terrain (stony heath, felsenmeer) supports lichen communities on the rocks and boulders, and turfey ericad/lichen heaths between boulders. Calcareous bedrock terrain is rare in the study region. The only calcareous rock terrain seen occurred locally along the upper Horton River, extending NE to the Melville Hills where *Dryas/Cetraria* tundras dominate.

Due to the concentration of rockland along the Shield--Paleozoic border, treeless uplands extend into the low subarctic region and southward into the high boreal (Figures 15A, B; cf. Figures 9A, B; 13A.1, A.2, B). Locally, cover of treeless uplands (due solely to rockland) actually increases southward, e.g., the area NW of the North Arm of Great Slave Lake. Ten to >25% of the terrain along the Shield--Paleozoic border between Great Bear and Great Slave Lakes supports treeless rockland.

Other regions of rockland are the East Arm of Great Slave Lake and parts of northern Saskatchewan. Elsewhere, rockland has little effect on the total cover of treeless uplands: south of the limit of trees, rockland cover is seldom >2%. North of the forest-tundra, rockland locally exceeds 10%, and even 25-50% NE of Takiyuak Lake; but these uplands would be treeless regardless of the harshness of the terrain.

4.3.8 Upland tundra, shrubland, and wetland combined.

Cover of "tundra" never reaches zero in the study region; only occasionally does "tundra" cover fall below 10%, even into the low subarctic and high boreal. At the southern edge of the study region, cover of this treeless vegetation is attributable to wetlands and shrublands, and less so to upland tundra in the highlands of the northwest. Depression contours highlight significant cover of trees, burned trees, rockland, and eroding terrain.

For the sake of brevity, combined upland tundra, shrubland, and wetland will be referred to as "tundra", with full knowledge that vegetation such as fen shrubland and treeless peat plateaus are not, strictly speaking, tundra. Cover of this treeless ground may be attributable primarily to climate or to abundant soil water.

Cover of tundra never reaches zero in the study region (Figures 16A, B) and only occasionally falls below 10%, even into the low

subarctic and high boreal. The apparent steep fall in tundra cover along the southern limit of the study region is an artifact and merely indicates the limit of the airphoto data. West of the Keith Arm of Great Bear Lake, tundra may exceed 25% due to bogs and shrubland in the lowlands, and to upland tundra and shrubland in the Norman Range (Franklin Mountains). The peak in tundra cover on Grizzly Bear Mountain is due both to upland tundra and to shrubland.

Relative to the contours for upland tundra, those for tundra lie noticeably farther south. This is most clear in the extreme southeast and northwest, where wetlands and shrublands occupy much of the terrain. In Keewatin, for example, the continuous 85% contour for upland tundra is not reached till north of the Henik Lakes, whereas for tundra, the 85% contour is reached in northern Manitoba.

Depression contours showing <85% in southern Keewatin, along the Thelon River, and on the Kendall River east of the Dismal Lakes highlight major groves of trees. These groves are evident as depressions on the tundra plateau in Figure 16A. Along the lower Horton, and between the lower Horton and Hornaday Rivers, depression contours highlight eroding terrain in picturesque Cretaceous badlands.

Extensive 10% depression contours SE of McTavish Arm, Great Bear Lake are due both to rockland and to trees. Northwest of Rocknest Lake on the Coppermine River, the 25% depression contour is due primarily to high cover of white spruce, and less so to rockland. The 10% depression contours east of Lac Maunoir on the

upper Anderson River, and at the big bend of the middle Anderson, are due to trees.

Depression contours near the northern Saskatchewan and Manitoba borders, near the Knife and Churchill Rivers, Manitoba, and at the southern edge of the Mackenzie Delta indicate high cover of trees or burned trees.

4.3.9 Upland tundra, shrubland, wetland, burned trees, and rockland combined

High cover of treeless ground extends across much of the southern edge of the study region. Wetland, rockland, and burns combine in three areas to produce pronounced southern peaks in treeless cover, highlighted by a *northward* fall in cover of treeless ground. Treeless ground drops below 10% only occasionally; such areas, where tree cover exceeds 90%, require a scarcity of rockland and low cover of burn.

In contrast to Figures 13A.1, A.2, B, and 14A, and B, which show cover of upland tundra determined solely by climate, Figures 17A and B depict the total cover of treeless ground without regard to origin or successional status. Climate, poor drainage, rockland, and fire combine to determine the overall cover of this treeless vegetation. The steep southern edge in Figure 17A is an artifact at the limit of data.

Most notable is the high cover of treeless ground across much of the southern edge of the study region. West of Keith Arm, e.g., treeless ground rises to >85% due mainly to burns and treeless bogs in the lowlands east and south of Mahony Lake.

Along the Shield--Paleozoic border between Great Bear and Great Slave Lakes, treeless ground fluctuates from 25-50%, due mainly to rockland and burns. Near the East Arm of Great Slave Lake, treeless ground peaks at >85% both south and north of the lake. South of the lake the peak is due to burn and rockland; north of the lake, the peak is due primarily to upland tundra.

In these three areas, viz., a) west of Keith Arm ; b) along the Shield--Paleozoic border; and c) in the vicinity of the East Arm of Great Slave; there is a pronounced "saddle" in the cover of treeless ground. Wetland, rockland, and burns combine to create southern peaks in treeless cover; northward, treeless cover actually falls for a short distance (where terrain and fire conditions favor dominance by trees). Thereafter, climatic controls exert their influences and treeless cover again increases. This saddle is most clearly seen on the contour map, Figure 17B; on the transect diagram, the saddle tends to be hidden by the southernmost peaks of treeless ground.

Treeless ground only occasionally drops below 10% cover anywhere in the study region. Such areas, where trees cover >90% of the landscape, require not only a favorable climate, but also a low cover of burn and scarcity of rockland. These conditions are met most often near the open crown forest/forest-tundra

transition NW of Great Bear Lake, and east of Great Slave Lake. Conversely, areas favorable for maximum tree cover are rare between Dease Arm (G.B.L.) and the East Arm (G.S.L.) due to prevalence of rockland and burns.

As in the previous "tundra" type, depressions in the treeless plateau of the transect diagram highlight other cover types. The large depressions are due to extensive tree groves, such as the Henik Lakes region of Keewatin and the Thelon River. Some small depressions in the northwest are due to eroding Cretaceous sediments in the badlands of the lower Horton River region.

The notch below the transect plateau in the northwest is located east of the mouth of the Kugaluk River. Here the gradient of vegetation change from treed to treeless communities is steep. Averaging of neighbor photos prevented reaching the 100% plateau (see Methods 3.2), although the terrain at the northern limit of the study region is 100% treeless.

4.3.10 Recently-burned trees

With some important exceptions, cover of burn ranges from 5-25% in the low subarctic, and from 0-10% in the forest-tundra. Fire exerts its greatest influence on the landscape in the northwest, where burns may approach the limit of trees. A NW--SE band of high burn cover is found north of Great Slave Lake. In the eastern half of the study region, burns extend only a short distance into the forest-tundra.

Due to the nature of burns, cover tends to vary widely, requiring more averaging to depict (eight neighbors; Figures 18A, B). Two other points are relevant to percent burn: (1) The figures depict only burned trees. (2) Old or slight burns, which showed evidence of fire but were currently treed were tallied under trees with the notation "includes old or slight burn", or other relevant data. In areas of slow tree regeneration or dysclimax, old burns would be classed as "recent" burn.

The bold line in Figure 18B depicts the approximate northern limit of burns. Actually this line describes the 1% level. A near-zero contour level could not be used as averaging at eight neighbors "pulls" the line northward, resulting in error. Northward of the bold line, <1% of the terrain is covered by fresh burn.

Inspection of Figure 18 indicates that burns exert their greatest influence on the landscape in the northwest. Treeless burns commonly exceed 25% cover; peaks of >50% are not uncommon. The largest amount of contiguous fresh burns extends SE of the Mackenzie River to the Colville Lakes.

Other peaks in burn cover are found north of the Great Bear River (west of Keith Arm); south of McVicar Arm, Great Bear Lake; NW from Indin Lake to Great Bear Lake, east of the Camsell River; and NW and SW of the East Arm, Great Slave Lake.

With some exceptions, burn cover in the low subarctic ranges from 5-25%, and in the forest-tundra, from 0-10%. In general, the amount of burned terrain increases southward, but regionally may peak farther north, e.g., between Great Bear and Great Slave Lakes

where 5-50% of the landscape in a NW/SE band is treeless due to burn.

In the eastern half of the study region, the approximate northern limit of burns generally extends only a short distance into the forest-tundra. In the northwest, where tree cover remains high well to the north, the limit of burns may approach the limit of trees, e.g., from NW of Sitidgi Lake to the mouth of the Kugaluk River. The observed pattern of burn in the northwest and elsewhere is discussed in section 5.4.

4.3.11 Shrubland plus recently-burned trees

A rough approximation of land dominated by tall shrubs is achieved when shrubland is summed with burn cover. These shrub-dominated lands reach their highest cover in the northwest.

Shrubs are often prominent as a stage in the regeneration of burned trees. In some cases, these shrubs may persist for many years, e.g., dwarf birch--blue green willow--green alder in the northwest. Where trees have been killed by fire, the young trees must pass through a stage where they are not distinguishable from shrubs on small scale airphotos. Summing shrubland and recently-burned trees gives a rough approximation of land currently dominated by tall shrubs, without regard to origin (Figure 19A).

Tall shrubs reach their greatest importance in the northwest. Shrubland in the Mackenzie valley and extensive burns elsewhere

keep the cover of tall shrubs above 50% for much of the area. Elsewhere along the southern fringe of the study region, burns are the prime source of tall shrubs, while shrubland fills in the matrix. An average cover in the southern part of the study region would be about 20%. To the north, burn generally decreases rapidly and shrubland gradually, usually not exceeding 1-2% at the northern limit of the study region..

4.3.12 Trees: introductory comments

Four approaches to mapping tree-cover are outlined.

In addition to climate, two other factors influence the landscape cover of trees at the regional scale. Rockland can be important in decreasing the amount of land suitable for trees, such as between Great Bear and Great Slave Lakes (Figure 9A). As well, fire decreases the total amount of land covered by trees at any given time. Thus, in depicting the areal cover of trees four distinct approaches were taken: (a) tree cover, unadjusted for rockland; (b) tree cover, adjusted for rockland; (c) tree cover plus burned trees, unadjusted for rockland; and (d) tree cover plus burned trees, adjusted for rockland.

At the (a) extreme, tree cover is shown at a minimum, as it existed at airphoto date on the landscape; terrain pre-empted by rockland is included in the denominator. At the (d) extreme, the maximum cover attainable by trees under the present climate is

depicted; areas treeless due to fire are considered treed, and the amount of rockland present is not included in the denominator. Under option (b), burns are not summed with trees, but rockland is not included in the denominator: this in effect factors out both burn and rockland. In (c), burned trees are summed with trees, but terrain pre-empted by rockland is included in the denominator: this option approximates the state where all fires are suppressed, but rockland still depresses tree cover.

Where fresh burns reach their greatest cover, principally in the low subarctic and southward, and where rockland is important, primarily between Great Bear and Great Slave Lakes, the four maps differ markedly. Elsewhere the maps are similar.

4.3.13 Trees, exclusive of burned, unadjusted for rockland

Tree cover is most noticeably depressed in the northwest where burns and treeless wetlands often attain high cover. Between Great Bear and Great Slave Lakes, maximum tree cover only once attains 85% cover due to the predominance of rockland and burns. East of Great Slave, tree cover often attains 85% before falling rapidly in the southern half of the forest-tundra. Locally complex gradients in burn, rockland, elevation, and wetland:upland ratio are reflected in the tree contours.

Low tree cover throughout much of the northwest is due primarily to fire (Figures 20A, B). West of Great Bear Lake, and

north of the Great Bear River, extensive burns and wetland reduce tree cover to <25 and even <10%.

Between Great Bear and Great Slave Lakes, much of the low tree cover is attributable to both rockland and burns. It is remarkable that tree cover only once attains 85% cover (in the middle stretches of the Wecho and Yellowknife Rivers). Tree cover west of the central meridian ($114^{\circ}45'W$) is noticeably depressed relative to that east of the meridian. Across much of the wide region westward from Great Slave Lake to the Yukon border, it is common for tree cover to rise for a short distance to the northward through the low subarctic. This surprising pattern is due to the combined effects of rockland, fire, and wetlands. In contrast, eastward from Great Slave Lake, tree cover often attains 85% before falling rapidly in the forest-tundra.

East of the central meridian, the general pattern is for tree cover to fall rapidly in the southern part of the forest-tundra. Thereafter, trees may extend some considerable distance northward before reaching their limit. In the west, the pattern of tree cover is less well-defined; cover often remains high until near the limit of trees and then drops precipitously. In Figures 20A and B this pattern is somewhat obscured by the effects of fires. West of the Anderson and east of the Mackenzie Rivers, e.g., tree cover falls erratically northward from maxima between >85 and 50% to zero (cf. Figures 22A and B where burn is included).

Tree cover in the Mackenzie valley and westward to the Cordillera is responding to complex and often sharp gradients of

wetland:upland ratio, elevation, and fire. As expected, tree cover values reflect these sharp gradients.

4.3.14 Trees, exclusive of burned, adjusted for rockland

Adjusting for rockland results in a substantial rise in tree cover in the central district east of Great Bear Lake and north of Great Slave Lake. Remaining depression contours in this district are primarily due to burns. In the northwest, rockland influences are limited to the Cordillera and NE of the Horton River, beyond the limit of trees. West of Keith Arm, treeless wetlands and highland tundras also depress potential tree cover. East of Great Slave Lake, only minor increases in tree cover appear after adjustment for rockland.

Figures 21A and B may be interpreted as the cover of trees, exclusive of burned, that would exist if rockland were removed from the landscape. The only clear differences between Figures 20 and 21 are found north of Great Slave Lake and east of Great Bear Lake, where rockland is extensive (Figures 9A, B).

Tree cover in this central district generally attains 85% before dropping northward due to climatic controls. Comparison of Figure 20A with 21A shows that the trough of low tree cover due both to burn and rockland in Figure 20A has risen considerably by removal of the rockland influence in Figure 21A. The plateau of $\geq 85\%$ evidently falls off again to the south. This may be

attributable to burn as will be seen in Figures 23A and B.

A deep depression contour still remains east of Hottah Lake, and locally SE of the East Arm, Great Slave Lake. Tree cover along the south shore of Great Bear Lake remains low, falling to <25% by McVicar Arm. These lows are due to fires. Depression contours on Grizzly Bear Mountain, and inland from Kokeragi Point on Keith Arm appear due to highland tundras. Farther inland from Keith Arm, and north of the Great Bear River, tree cover is variable, indicative of burns, treeless wetlands, and the Norman Range SW of Mahony and Kelly Lakes.

East of Great Slave Lake, only minor increases in tree cover appear after adjustment for rockland. Notable increases are more or less restricted to the area around the East Arm of Great Slave Lake. The forest-tundra region east of Great Slave Lake is clearly not as rocky as that to the north.

Rocky terrain may be found elsewhere in the study region, such as high in the Cordillera, NE of the Horton River, and NE of Takiyuak Lake, but these lie beyond the limit of trees.

4.3.15 Trees plus recently-burned trees, unadjusted for rockland

Burns exert a profound effect in depressing tree cover in the northwest, especially west of Keith Arm, and between the Colville Lakes and the Mackenzie River. Between Great Bear and Great Slave Lakes, both burns and rockland depress tree cover; north of the 50% tree contour, burn and rockland effects are insignificant. East of Great Slave Lake, burns exceed rockland in their effects on tree cover.

When burn is summed with trees, the areas west of Keith Arm and south of McVicar Arm, Great Bear Lake, show a dramatic rise in tree cover in Figures 22A and B (cf. Figures 18, 20). Much of the terrain west of Keith Arm now lies above the 85% contour for tree cover; areas still lying below the 85% contour are due to treeless wetlands. Southwest of Kelly Lake, bordering on the Mackenzie River, the area lying below the 50% contour is due to upland tundra, shrubland, and a small amount of rockland in the Norman Range.

A rise in tree cover is also seen in the Colville Lakes region. With the exception of the areas around Lac des Bois and west of Lac Belot, most of the area rises above 85% tree cover when burn is included. The remaining irregularity in the 85% contour is due to large wetlands (mostly peat plateaus).

From northwest of the Colville Lakes to the Mackenzie River,

the inclusion of burn converts a bewildering system of contours in Figure 20B to an easily readable one in Figure 22B. On the transect diagrams this is indicated by an extremely bumpy surface in Figure 20A, which is made less so when burns are included under tree cover. Clearly, fires exert a profound effect on tree cover in the northwest.

Figure 21 shows a peak in tree cover east of McTavish Arm, Great Bear Lake; Figure 22 shows no such peak, demonstrating that rockland is depressing the potential tree cover there. In the SE cove of McTavish Arm, a depression contour in Figure 22B highlights a sharp fall in tree cover. The contour is misleading in that the eastern half of Richardson Island is excluded; this is an inaccuracy of the automated mapping. Much of Richardson Island rises 305 m above Great Bear Lake to rocky summits. Tree cover (unadjusted for rockland) reaches only about 45%, and rockland about 40%. Although this area was classed as open crown forest region, valid upland tundra may be present on some summits.

Elsewhere, between Great Bear and Great Slave Lakes, tree cover has risen in some areas and dropped in others when Figures 21 and 22 are compared with Figure 20. These changes are most evident with the 85% contours, although some change is observable down to 50% cover. North of the 50% contour, both burn and rockland cease to be important factors in depressing tree cover.

East of Great Slave Lake, inclusion of burned trees with trees has a larger effect in elevating tree cover than does correcting for rockland (cf. Figures 20, 21, 22). Between Great Slave Lake and Hudson Bay, when burn is excluded and tree cover is adjusted for

rockland (Figure 21), maximum tree cover often does not attain 85%. In contrast, adding burn to tree cover, but not adjusting for rockland, results in generally higher tree cover and a more continuous 85% contour. Clearly, burn exceeds rockland in its effect on tree cover in the subarctic east of Great Slave Lake.

The depression contours found in the East Arm of Great Slave Lake in Figure 22B do not appear in Figure 21B, where tree cover is adjusted for rockland. In contrast, some depression contours around the East Arm in Figure 21B do not appear in Figure 22B. On the peninsulas and islands in the East Arm, rockland seems to be more important than burn in depressing tree cover. Around the lake, the situation is reversed and burns exert their influence. North from McLeod Bay, however, tree cover rapidly drops below 50% and burns cease to have an appreciable effect on the vegetation. Tree cover north from McLeod Bay is limited both by rockland and, increasingly to the north, by climate.

4.3.16 Trees plus recently-burned trees, adjusted for rockland

Topoclimatic and terrain influences are indicated in the observed patterns of tree cover in the forest-tundra. High elevations, acidic crystalline bedrock, coarse-textured soils, and thin surficial cover correlate with low tree cover; low elevations and fine-textured soils over sedimentary rocks correlate with high tree cover.

Figures 23A and B present potential tree cover as might exist in

the absence of burns and rockland. Such a depiction should show a better correlation with climate than that possible in Figures 20-22. Major discontinuities in percent cover of trees should then be attributable to discontinuities in climate, elevation, drainage, parent material, or history. This section highlights some local and regional topoclimatic, vegetation, and terrain relationships with case studies. Synoptic relationships are considered in Discussion 5.2.

An inlier of low arctic is located in the Caribou Hills east of the middle Mackenzie Delta. The absence of trees is likely topoclimatic. Near the mouth of the Kugaluk River, tree cover falls from >50 to 0% in about 10 km, perhaps due to a steep climatic gradient caused by the proximity of cold marine waters.

The steep fall in tree cover SSE of Sitidgi Lake is difficult to explain. Tree cover falls to a minimum of 12% and lichen-rich upland tundra rises to 80%. Mean elevation at the tree cover minimum is 260 m, about 50 m above the surrounding 10 sample photos, and unlikely to exert a topoclimatic effect. Bedrock is homogeneous: upper Devonian sandstones and shales. It is possible that fire history plays a role here. Nearby, there are large burns, including some of upland tundra. Perhaps Tong absence of fire in the area SSE of Sitidgi Lake resulted in extreme tree thinning with the development of upland tundra.

In the absence of fire in the northwest, tree stands may undergo a progressive decline in tree density (Black 1977). Following fire and disturbance of the organic mat, the active layer may be greatly thickened on these fine-textured soils. The warmer soil, with an

increased supply of liquid water encourages a dense growth of tall shrubs and spruce, lending these communities a dark airphoto tone. With eventual re-establishment of the vegetation mat, the active layer thins and tall shrubs and trees decline in density. Frequently the trees, dwarf birch, willow, and alder become restricted to runnels with lichen dominated interfluves. In the northwest, it is often difficult to decide whether lichen-dominated interfluves are better classed as upland tundra or as an interfluve matrix in a sparsely treed stand.

Elsewhere, north of Great Bear Lake, midway between Dease and Smith Arms, tree cover falls from 85 to <25% in about 12 km. The steep fall in tree cover occurs at the Big Spruce Hills which rise to over 535 m, over 365 m above the level of Great Bear Lake. North of the Big Spruce Hills, tree cover falls from >50 to <2% in 15-25 km. Here elevation rises to the north and east by about 150-230 m to an extensive coarse-textured outwash plain. The combined effects of elevation and a rapidly-drained and exposed outwash plain are enough to bring white spruce cover to near zero. Northward from the outwash plain, elevations fall about 75 m, Horton Lake and Horton River are reached, and white spruce cover rises to about 25%.

North of the east end of Dease Arm, tree cover falls from >50 to 0% in 20-30 km. Again, a steep topoclimatic gradient probably accounts for the fall. Elevations rise over 300 m from Great Bear Lake to 460 m, and continue to rise north of the limit of trees (white spruce).

To the east, the central third of the Dismal Lakes lies beyond the limit of trees. White spruce extends NE from the Dease River area to

the westernmost Dismal Lakes. The northernmost spruce occur here in poorly-drained terrain a few km north of the lake and south of a prominent scarp.

White spruce also extends NW up the valley of the Kendall River to the easternmost Dismal Lakes. From the central Dismal Lakes a treeless peninsula extends south to a wide area lying generally above 600 m. Tree cover increases in all directions down from this highland, especially to the south and west where values >50% are met in as little as 20-30 km.

West of the middle Coppermine, and north of Hepburn Lake, tree cover falls abruptly from >50% to near zero before rising rapidly northward into the valley of the Coppermine. The area of minimum tree cover lies 30-75 m above the surroundings, perhaps sufficient to depress tree cover (a climatic threshold is passed?). Bedrock is complex in this area with paraschists and paragneiss, a variety of sedimentary rocks, granitic gneisses and related rocks, and volcanics. It is likely that acidic crystalline rocks, with perhaps a thin surficial cover, dominate where the tree cover is lowest.

The entire area lying north of Snare Lake, between the Coppermine River and McTavish Arm of Great Bear Lake, presents fascinating changes in vegetation and landscape (Figure 23C). For example, on a line north from Snare Lake (beginning ~5-10 km west of Snare Village) extending to the Coppermine River north of Rocknest Lake, the following relevant changes take place: (a) mean elevation rises from ~375 m at Snare Lake to >450 m midway between Snare and Rocknest Lakes, then falls again to ~400 m by the valley of the Coppermine; a maximum elevation of >520 m is reached before dropping into the

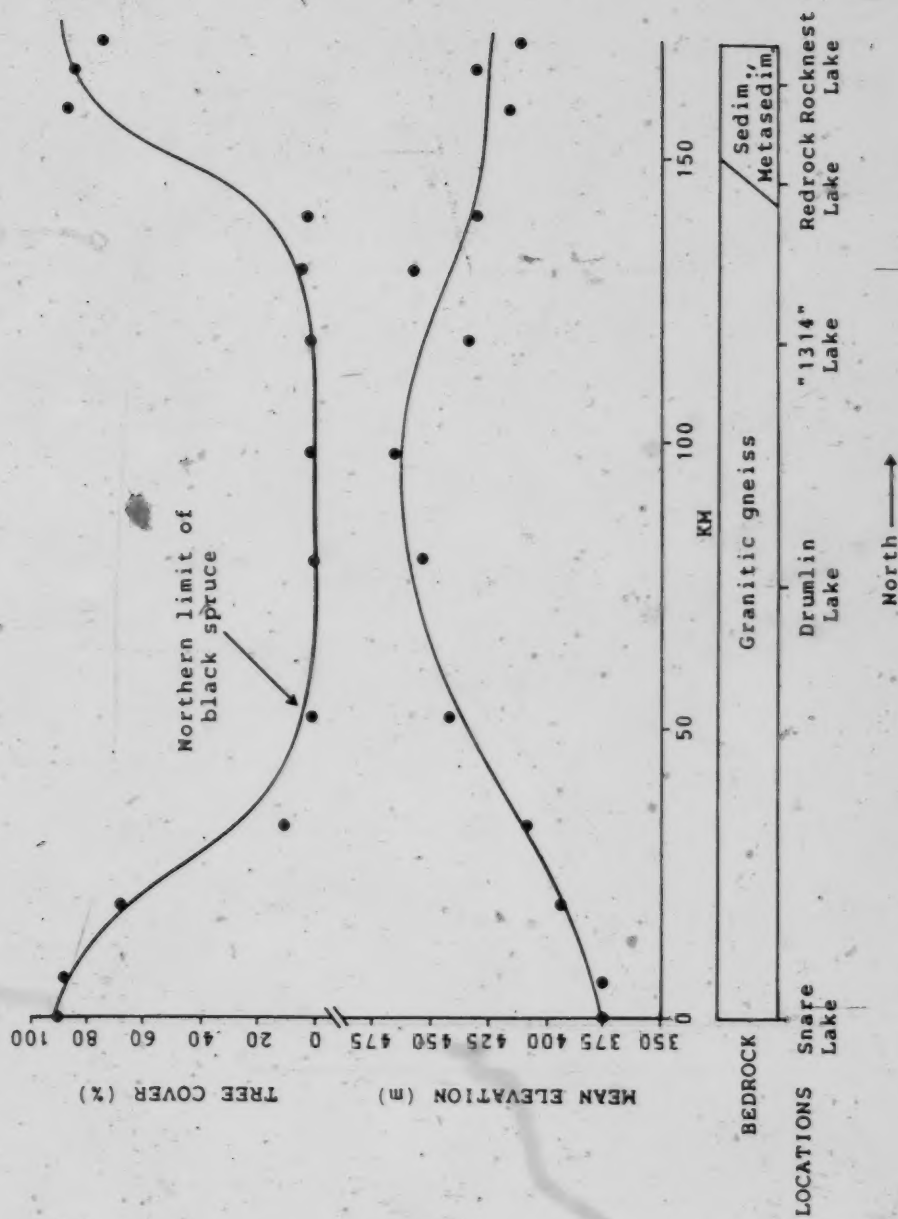


Figure 23C. Tree cover, mean elevation, and bedrock changes on a south to north transect between Snare and Rocknest Lakes. Longitude ca. $114^{\circ}15' W$.

Coppermine; (b) bedrock is predominantly Archean acidic rocks, principally granitic gneisses, but changes to a complex of many rocks (mostly sedimentary) by the valley of the Coppermine; (c) soils at Snare Lake are sandy brunisols with a pH of 5-6 in the Bm horizon; soils along the Coppermine River north of Rocknest Lake are silt loam gleysolic cryosols with a pH of 8; (d) predominant vegetation at Snare Lake is a moist black spruce/dwarf birch--ericad woodland; white spruce is dominant only on glaciofluvial sands; occasionally black and white spruce form mixed stands on mesic to dry-mesic soils; bog-fens and peat plateaus occupy lowlands, (peat plateaus are scarce north of Snare Lake); (e) predominant vegetation on the Coppermine River north of Rocknest Lake is a rich white spruce/dwarf birch/shrub/*Tomenthypnum*--*Rhytidium* forest with many calciphiles; white spruce is the only tree species present; (f) along this line, tree cover drops from >85% (including burns, or from about 50% if burns are excluded) at Snare Lake to 10% in about 10-27 km, and then to 0.6% at only 50 km north of Snare Lake; at about this location, black spruce disappears from the landscape; northward, white spruce is the sole tree and it thins to 0-0.3% from south of Drumlin Lake to north of "1314" lake on the highland south of Redrock Lake; (g) at about 12 km south of Redrock Lake, white spruce begins to increase in cover (Plate 1); at the south shore of Redrock Lake, white spruce increases rapidly; (h) by the narrows between Redrock and Rocknest Lakes, white spruce occupies >70% of the landscape, and maintains this high cover well to the north.

Tree cover extends a remarkable distance eastward from McTavish

Arm of Great Bear Lake, to the north of Point Lake and west of Takiyuak Lake. Indeed, from Takiyuak Lake south to Point Lake, the limit of trees lies virtually north-south, with high cover extending a short distance beyond the valley of the Coppermine. Elevation rises steeply at first from 156 m on Great Bear Lake's shore to 300 m, then increases to 380 m. An intervening highland is reached where mean elevation exceeds 450 m, thence elevation drops again as the Coppermine valley is reached. In the Coppermine valley, local relief often exceeds 150 m, with minimum elevations of 300-375 m and maximum elevations of 500-600 m. East of the Coppermine, trees do not rise above 450 m elevation.

Tree cover in this area shows some apparent correlations with the bedrock. Locations having high tree cover, in general, are underlain by carbonates, slates, greywacke, conglomerates, other sediments, and their derived schists and gneisses. Areas of low tree cover, in contrast, are frequently underlain by acidic granitic gneisses and related crystalline rocks and volcanics. Farther south, at Winter Lake and southward, where the underlying bedrock is granitic gneisses and related, black spruce dominates forest-tundra-tree communities; white spruce is usually restricted to glaciofluvial deposits and local circumneutral soils ($\text{pH} \geq 6$).

In the eastern half of the high subarctic, there are two major discontinuities in tree cover: the Thelon River and south-central Keewatin. Details relating to the Thelon, south-central Keewatin, and other areas are discussed in 5.2.4.

In brief, the lower Thelon occupies a broad valley underlain by sedimentary rocks, sloping gradually upward to the surrounding

plain. In contrast, the upper Thelon occupies a shallow valley underlain by granitic gneisses; tree cover ranges from 0-5%. Treeless areas occur south of the big bend of the Thelon, and SW of Sid Lake; tree cover (white and black spruce, and larch) here has fallen to about 0.2%.

By the Thelon's middle reaches, north to the Hanbury River, elevations have fallen considerably; surficial material is derived from deep-lying Proterozoic sandstones and related rocks; tree cover varies from 0-2%. Northeastward, mean elevation drops well below 150 m, reaching a minimum of about 90 m at the northern limit of trees. Tree cover rises to a maximum of 20%, then falls to 2% by the confluence of the Tamarvi River at the Ursus Islands. The limit of spruce is reached about 10 km upstream from Beverly Lake.

In south-central Keewatin, the striking pattern is the remarkably gradual fall in tree cover once it has dropped below 10%. The continuous 10% contour in the SE skirts the north end of Ennadai Lake, extending northward both in the valley of the Nowleye and Kazan Rivers north of Ennadai; east of the Kazan River, the 10% contour drops south some 100 km, then east, crossing Nueltin Lake near its north end, dropping below 60°N about 50 km west of Nejanilini Lake. From 60°N, the 10% contour drops south some 45 km, then east, past the south end of Nejanilini Lake. At Nejanilini Lake, the uplands are apparently dominated by a typical Shield tundra association of dwarf birch/ericad/lichen; lakeshores and depressions support black spruce and larch with dwarf birch and *Salix planifolia*, sedges, and cottongrass; paper birch is present; the vascular flora is composed of about 83 species, relatively poor in comparison to

Nueltin Lake (~134 species) and the Churchill area (~366 species) (Scoggan 1952). The vegetation and flora of the eastern side of Baralzon Lake (~98° 10'W, 60°N), about 70 km NNW of Nejanilini Lake, was described by Scoggan (1952).

The 10% tree cover contour trends ESE from Nejanilini Lake for about 110 km, turns SE across the Seal River some 15 km upstream of the big bend of the Seal, then crosses the Churchill River about 80 km south of Hudson Bay, and leaves the study region.

North of this 10% contour, the forest-tundra extends a great distance to the north before the limit of trees is reached. Tree limit is met most rapidly NNE of Ennadai Lake in 65-70 km. Commonly the distance from the continuous 10% contour to zero trees exceeds 190 km. At its widest, from north of Great Island on the Seal River, to west of Kinga Lake, this transition takes place over 280 km!

Extensive "groves", where tree cover exceeds 10% are found between Kamilukuak Lake and Kazan River, and in the Henik Lakes area. In the Kamilukuak--Kazan "grove", black spruce, larch, and white spruce are all present, typically in a matrix of tall shrubs. Tree cover reaches a maximum of about 25%, and averages 15-20%; cover decreases rapidly outside this area, especially to the NE, where cover may fall from 10% to zero in as little as 12 km.

Farther east, the Henik Lakes grove, delimited by an area where tree cover exceeds 10%, spans 60 km N--S and 120 km E--W. Low tree cover appears associated both with higher elevations and with granitic and related gneissic bedrock; high tree cover appears associated with lower elevations and bedrock of greenstones, and also greywacke and metasediments. Black spruce, white spruce, and larch

are all present and occur on wet to moist slopes, shores, and depressions, often in a tall shrub matrix. Some extensive groves of larch stand out clearly due to their light crowns. Tree cover peaks at about 25%.

Between these areas of high tree cover, and north of Nueltin Lake, lies an area where tree cover falls below 2%. That area, centered south of Watterson Lake, is underlain by acidic granitic gneisses, often only thinly covered with a veneer of till. Spruce and larch are restricted to drainages, depressions, and lakeshores, often in a tall shrub matrix.

4.3.17 Ratio of percent cover of trees:upland tundra

The forest-tundra spans an average 150 km (± 75 km); in the western half of the study region, the forest-tundra spans 112 ± 41 km, and in the east 186 ± 81 km. On average, the forest-tundra increases in width from northwest to southeast. The 100:1 to 1:100 trees:upland tundra cover transition comprises 90% of the area of the forest-tundra; the 10:1 to 1:10 band occupies 25-55% of the forest-tundra.

In Figure 24, both tree and upland tundra cover values are adjusted for rockland, and tree cover includes burned. The inclusion of burns and adjustment for rockland was done to emphasize climatic correlation in the tree:upland tundra ratio. Use of this ratio also tends to factor out the effect that wetlands have in decreasing the

cover of both upland tundra and tree communities. The $\log_{10}$ of this ratio plus 3.0 is depicted in Figure 24; a value of zero for the transformed ratio is equivalent to a cover ratio of 1:1000 trees:upland tundra and 6 is equivalent to a ratio of 1000:1 trees:upland tundra. The 20 kly yr^{-1} net isorad (after Hare and Hay 1974) is overlaid for climatic comparison in Figure 24B.1. See Appendix 2 for details of calculations.

Hachured closed contours on Figures 24B.1 and B.2 denote an increase in upland tundra cover relative to trees. In the case of the Churchill River, the hachured contour denotes a steep drop in tree cover due to wetland. Bold lines north of the forest-tundra denote tree groves. The plateau on the transect diagram denotes the 1000:1 tree:upland tundra ratio, and the plain the 1:1000 ratio. Depressions below the surface of the plateau denote outliers of upland tundra south of the contiguous forest-tundra.

Figure 24B.1 is a simplified version of Figure 24B.2. The limits of tree and upland tundra vegetation are used here as the cardinal criteria delimiting the forest-tundra. These are shown in bold lines. The narrow line between these limits denotes the location where tree and upland tundra cover are equal.

Those who disagree with using absolute limits of trees and upland tundra as boundaries for the forest-tundra might wish to apply narrower ratios. Use of rational limits of 1:100 and 100:1 (lines 1 and 5 in Figure 24B.2), for example, would narrow the contiguous forest-tundra by about 10% (range 2-60%) and cut off the middle Thelon River from the contiguous forest-tundra. In other words, the 1:100 to 100:1 band spans about 90% of the forest-tundra.

Boundary limits for tree:upland tundra cover of 1:10 and 10:1 (lines 2 and 4 in Figure 24B.2) would narrow the forest-tundra by an average 45-75%; i.e., this band occupies 25-55% of the forest-tundra. This narrowly bounded forest-tundra would range in width from about 30-75 km from east of the Mackenzie Delta to the NE side of Great Bear Lake; 20-95 km from NE of Great Bear Lake to the East Arm of Great Slave Lake; 20-70 km from the East Arm to west of the Dubawnt River; 40-100 km from the Dubawnt River to central Keewatin--Manitoba; and 40-55 km in NE Manitoba (outside of the Hudson Bay Lowlands). In the description to follow, ratios of 1:1000 and 1000:1 trees:upland tundra are used to delimit the forest-tundra.

The forest-tundra transition zone (exclusive of the Cordillera, Mackenzie Delta, and Thelon extension) averages 150 km wide but varies greatly (S.D. ± 75 km, N=36). In the western half of the study region, from east of the Mackenzie Delta to north of Yellowknife, the forest-tundra spans 112 ± 41 km (N=18); the eastern forest-tundra spans 186 ± 81 km (N=18). Regional minima are reached on the lower Anderson River (47 km), at Dease Arm (Great Bear Lake), and the East Arm (70 km); greatest widths are found between the Dubawnt River and central Manitoba--Keewatin (235-345 km). The forest-tundra on average increases in width from northwest to southeast; the western forest-tundra spans only about 0.6 the width of the eastern forest-tundra. The increase in width is most evident between Great Slave Lake and central Manitoba-Keewatin.

4.3.17.1 The northern limit of trees

The northern limit of trees is detailed with reference to airphoto data, field observations, and other studies.

At the northwestern extreme of the study region, the northern limit of trees is fragmentary along the east slope of the Cordillera (Figure 24). Here treeline is primarily a function of elevation, and as each sample photo covers a minimum of 130 km^2 , both high and low elevations occurred on each photo. When these data "points" are averaged, tree cover contours fail to express the sharp vegetation gradients.

Eastward, treeline reaches Shallow Bay in the Mackenzie Delta, and swings east to near Tununuk, south of Richards Island. On Tuktoyaktuk Peninsula, the limit of trees drops SE to the west end of the Eskimo Lakes, parallels the south shore of the Eskimo Lakes about 10 or more km inland, then reaches the shore of the Eskimo Lakes again at the mouth of the Kugaluk River. Eastward from the Kugaluk River, the limit of trees crosses the Anderson River at $69^{\circ}20'N$ and the Horton River at $69^{\circ}30'N$ (Plate 5). The forest-tundra limit then parallels the Horton River SE beyond Horton Lake, then swings eastward north of Dease Arm, Great Bear Lake.

Prest (1985) noted the northernmost spruce (white?) he observed north of Dease Arm and south of Bebensee Lake. They grew alongside a large aufeis on a seemingly unprotected knoll at $67^{\circ}21'N$ and $118^{\circ}19'W$ and 370 m elevation. The "treeline" according to Prest lies some 10 km south of these coordinates and below 290 m elevation.

"...Here, near a lake with an elevation of 259 m, spruce trees are relatively common with heights of 5 to 7 m... and a diameter of 10 to 12 cm a metre above ground. But interspersed with these and on higher tree-free ground, there are old weathered stumps and logs up to 30 or 35 cm in diameter. These observations indicate a modern climatic deterioration." (Prest 1985:63)

Passing to within 20-25 km of the north shore of Great Bear, the limit of trees turns slightly north of east and reaches the westernmost Dismal Lakes. Near the west end of the Dismals, treeline dips sharply southward due to a highland south of the lakes, then returns north to the east end of the Dismals. Extending eastward about 10 km north of the Kendall River, white spruce reaches the Coppermine Valley and extends north to about Escape Rapids at 67°35'N. Here treeline turns south, then for a short distance swings east up Melville Creek, and returns to the Coppermine River at ~66°45'N.

Trees evidently extend north of Escape Rapids. Jenness (1928:70) wrote:

"... the most northerly stand of timber lies in the valley of a small creek six miles from the sea and three or four miles from the actual river-bed (of the Coppermine); south of this, groves of spruce, mingled with a little cottonwood [*Populus balsamifera*?], appear at intervals of every mile or two, the groves becoming larger, and the trees bigger, as one travels upstream. All the bigger trees in the northernmost groves are dead, and many of the smaller ones have dead and withered branches, so that the timber-line seems to be moving southward."

Jenness' biologist companion, Johansen, collected seven species of wood and bark-boring beetles from living, dying, and dead wood near the limit of spruce on the Coppermine, among them *Dendroctonus johanseni* (Swaine 1919; Johansen 1921, 1924; Holm 1922). The apparent southward movement of the tree limit may have been brought

about in part by the beetles, but this question has not been studied since.

During fieldwork in the Kendall River--Dismal Lakes area we observed large tracts of dead white spruce. In a few places, entire forests had succumbed and the bleach-white boles lent a stark beauty to the slopes, while in others individual trees or clones had died resulting in less dense stands. Data are insufficient to age this die-off or to determine its duration. About half the trees aged in this area (31 of 56) fell into the 51-100 yr class at breast height; ages near ground level ranged between 116-273 yrs (N=5), and below-ground ages 255->390 yrs (N=4). Seedlings and transgressives were present but too rare in the tree stands studied for accurate estimates of density. Sapling density (including clonal stems) was 391/ha and tree density was 106/ha in representative stands. By virtue of (a) the observations of Jenness (1928) and Johansen (1921, 1924), (b) the apparent antiquity of the abundant deadwood, and (c) the fragmentary age data, it appears the die-off in this area may have taken place during the Little Ice Age (~1600-1850), perhaps even earlier. The rarity of young white spruce in tree stands suggests they have not responded to the early twentieth century warming.

A similar(?) mass mortality of old-aged black spruce trees took place in a stand near treeline in northern Québec between 1880-1890 (Payette et al. 1985). The authors attributed the mass death to inability of senescent and moribund trees with limited photosynthetic potential to take advantage of the warmer conditions following the Little Ice Age.

From the Coppermine, tree limit trends SE to the west arm of

Takiyuak Lake, then near its SW shore, and south to west of Rockinghorse Lake. Curving SW to Point Lake, treeline turns SE irregularly then north a short distance to Lake Providence. Dropping straight south by the west end of Jolly Lake, treeline turns east along the south shore of Courageous Lake. Somewhere between Little Marten and Courageous Lakes, black spruce makes its first unequivocal appearance at the northern limit of trees (Plate 6).

Turning SE across Mackay Lake, east of Warburton Bay, tree limit winds its way by Lake of the Enemy then past Back and Walmsley Lakes to near the north end of Artillery Lake. Dropping south, west of Campbell Lake, treeline turns ESE, skirting the north end of Whitefish and Lynx Lakes before turning north down the valley of the Thelon.

Treeline passes by the east shore of Tyrrell Lake, then crosses the Hanbury River near its big bend before it empties into the Thelon. In the sector between about Little Marten Lake and the Hanbury River, black spruce apparently predominates at the limit of trees. At the Thelon, white spruce returns to dominance in the tree communities. Paralleling the Thelon River closely along its north side, trees extend north into the Tammarvi River grove west of the Ursus Islands. The NE limit of spruce in the Thelon is reached about 10 km upstream of Beverly Lake.

Trees (primarily white spruce) extend irregularly SE from the Thelon along a number of tributaries. Chief among these, from NE to SW, are: Kigarvi River and Spruce Grove Lake; Finnie River; a grove west of the Finnie River; an unnamed river east of Clarke River (which enters the Thelon near Hornby Point); and the Clarke River.

Upstream of Clarke River, the limit of trees returns to the Thelon proper and turns south near the west shore of Beaverhill Lake.

Tree limit then passes into the Dubawnt watershed at the NW end of Sid Lake, where both black and white spruce are found. Turning NE by the north shore of Mary Lake and the NE side of Mosquito Lake, treeline passes east across the Dubawnt River and the south shore of Dubawnt Lake. Tree limit then turns south past Carruthers Lake to Angikuni Lake on the Kazan River, then eastward by the north side of North Henik Lake.

From North Henik Lake, treeline continues east to Kinga Lake. Eastward from Dubawnt to Kinga Lakes, white and black spruce and larch are all present at the northern limit of trees with local variations in importance. It is possible that white spruce extends slightly farther north than the other two conifers, but more work is required before such a statement could be made with certainty.

From Kinga Lake, tree limit drops SE through eastern Keewatin and reaches the shore of Hudson Bay in northern Manitoba slightly north of the mouth of the Caribou River. East of the Churchill River, the limit of trees is once again reached inland from Cape Churchill, Manitoba. White spruce is dominant at the limit of trees near Churchill (Scott et al. 1987b).

Tree groves are only rarely isolated from one another by more than a few km. On a small-scale depiction of the forest-tundra such as Figure 24, these groves are contained within the boundaries of the contiguous forest-tundra. Only a few groves are isolated and/or large enough to be plotted as distinct outliers in an averaged plot.

East of Great Slave Lake, four such isolated groves are plotted in Figure 24B. From west to east these are: (a) south of Aylmer Lake, 0.1% tree cover, in tall shrub matrix, probably black spruce; (b) north end of Artillery Lake, 0.3% cover, in tall shrub matrix on shores and drainages, probably black spruce; (c) Williams Lake, west of Tyrrell Lake, 0.3% cover on esker--outwash margin, as white spruce; (d) Kazan River, south of Yathkyed Lake, 0.3% cover in valley of Kazan (observed on airphoto); west of the Kazan River, Larsen (pers. comm.) observed on the ground, a spruce stand NW of the shore of an unnamed lake at $98^{\circ}37'W$ and $62^{\circ}33'N$; some of the spruce had been cut down some time previous with a dull axe, and the stumps at the base measured about 15-20 cm in diameter.

Other tree groves are concealed in the averaging required to generate the maps. Some of these outliers are evident in Figure 1, such as eastward from Mackay Lake to the Thelon River.

4.3.17.2 Occurrence of black and white spruce at the northern limit of trees, with emphasis on the northwest

White spruce is the dominant, if not the sole, tree of the northern forest-tundra eastward from the Mackenzie to the Coppermine River. The transition from white to black spruce dominance at the northern limit of trees occurs near a major landscape--climatic transition north of Great Slave Lake.

Black spruce is apparently rare or absent at the northern limit of

trees in the northwest, and indeed throughout most of the forest-tundra there. From south of Point Lake, extending down the Coppermine River, westward up the Kendall River to the west end of the Dismal Lakes (NE of the Dease River), and again where trees were observed in the landscape east of Horton Lake, and extending the entire length of the Horton River, black spruce is absent (field observ.). White spruce is the only tree present across this entire region (occasional clones of balsam poplar on alluvium and trembling aspen on steep south- or west-facing slopes were observed along the Horton River; these never exceeded 2.5 cm dbh or 3 m ht). Similar shrubby clones of balsam poplar and trembling aspen were observed by Jenness (1928) and others of the Canadian Arctic Expedition in the valley of the lower Coppermine (north of Sandstone Rapids).

Black spruce is evidently rare in the northern forest-tundra westward to at least the Kugaluk River and beyond. Zoltai et al. (1979) noted only one occurrence of black spruce in the entire region lying between 122° and 131°W. Similarly, they found that larch was rare but constant in the SW of their study region (south of the Crossley Lakes). Balsam poplar and aspen were restricted to the valleys of the Anderson and Horton Rivers, apparently as occasional small-stemmed clones (on steep south- or west-facing slopes). Paper birch was noted by them on similar valley slope sites between Fort Anderson (Anderson River) and the Carnwath River.

Westward to the Mackenzie River, white spruce is by far the dominant tree, and often the sole tree species in the forest-tundra. In the Mackenzie Delta, white spruce grows on the highest ground; slightly lower ground is dominated by balsam poplar, followed below

that by alder (*Alnus crispa*) thickets, and below that by alder--willow or willow thickets (*Salix alaxensis*, *S. farriar*, *S. pulchra*). Balsam poplar extends farther north than white spruce in the Delta, reaching both east and west of Shallow Bay and forms the limit of trees (Mackay 1974). Both black spruce and white spruce individuals and clones are found on the Tuktoyaktuk Peninsula well beyond the limit of arborescent ($\geq 3-4$ m) trees (Ritchie, pers. comm.).

Elsewhere in the west, black spruce occurs on Great Bear Lake (cf. Lindsey 1952), but whether or not it is important in the forest-tundra east of McTavish Arm, or north of the lake is not published.

The dominance of white spruce in the forest-tundra of the northwest is noteworthy in that black spruce is better adapted to fire than is white spruce (Rowe 1970; Black 1977), and that fires exert a more profound effect on the forest-tundra of the northwest than elsewhere (see Discussion 5.4).

In the eastern half of the study region, black spruce is relatively abundant at the limit of trees, making its first unequivocal appearance at the tree limit somewhere between Little Marten and Courageous Lakes, and remains important southeastward. With few exceptions, e.g., the Thelon River area (see Clarke 1940), and the vicinity of Churchill, Manitoba (see Scott et al. 1987b), black spruce appears areally-dominant over white spruce.

The transition from white to black spruce dominance parallels a major landscape discontinuity from fine-textured relatively nutrient-rich loams in the northwest to nutrient-poor acidic sandy

loams and loamy sands of the Shield. This landscape transition similarly forms the boundary between distinct forest-tundra sub-regions with characteristic vegetation and climate. These topics are explored in Discussion 5.2.

4.3.17.3 The southern limit of upland tundra

The southern limit of upland tundra is detailed with reference to airphoto data and field observations. Most outliers of upland tundra are found in the highlands of the northwest.

The southernmost bold line in Figure 24B depicts the 1000:1 tree:upland tundra ratio and may be interpreted as the southern limit of the forest-tundra.

West of the Mackenzie Delta, upland tundra reaches its lower elevational limit at the lowest slopes of the Cordillera, paralleling the Mackenzie Delta to its mouth. Due to averaging, the limit of upland tundra turns eastward across the base of Shallow Bay in the Delta, and drops SSE past Inuvik. In reality there is virtually no upland tundra habitat in the Mackenzie Delta proper, as the "uplands" such as levees typically support tall shrubs or trees. Eastward from the Delta, however, upland tundra rises to dominate the landscape. Because of this steep gradient in upland tundra, the averaged contour line is "pushed" westward into the Delta.

South of Inuvik, the southern limit of upland tundra turns SSE west of Campbell Lake, then eastward south of Caribou Lake for about

170 km. In this area, the southern limit of upland tundra is the least definite of anywhere in the study region. Characters related to fire history such as soil drainage, succession and sub-climaxes, and progressive tree stand thinning, make identification of upland tundra at its southern limit somewhat equivocal.

At about 130° W, the upland tundra limit turns northward for 35-40 km, then eastward about 60 km to the Anderson River. Tundra cover drops in the Anderson valley proper, causing the southern limit to "V" northward. Crossing the Anderson River again west of Tadenet Lake and north of Simpson Lake, the southern limit drops steeply southward past Simpson Lake to the north shore of Aubry Lake and thence past Colville Lake and Lac de Bois. From Lac de Bois, the southern limit of upland tundra crosses the headwaters of the west branch of the Anderson, then winds southward to the north shore of Smith Arm, Great Bear Lake. There may be valid upland tundra SE of Lac des Bois, for maximum elevation rises to 440 m there, but no sample photos covered this topographic rise.

Crossing to the south shore of Smith Arm, the southern limit contour drops SE of Mackintosh Bay, past Deerpass Bay, then curves around the highlands near Kokeragi Point. The presence of upland tundra both in the Scented Grass Hills east of Mackintosh Bay and the highlands SW of Deerpass Bay is due to elevation. The Scented Grass Hills rise to 600 m, 450 m above Great Bear Lake. Southwest of Deerpass Bay, the highlands peak at about 520 m; here upland tundra cover is about 5%, but the actual cover may be higher as photo quality was poor and an unusual-looking shrub vegetation (due to burn?) occupied much of the uplands.

Eastward, upland tundra is absent at Cape MacDonnell at the tip of Takaatcho Peninsula, Great Bear Lake. Southeast of Takaatcho, the continuous southern limit of upland tundra turns SE from near Port Radium, McTavish Arm. In the forest-tundra around Hornby and Norrie Bays, McTavish Arm, white spruce is the dominant tree; black spruce is confined to "muskegs", and paper birch is present; edaphic lichen and low shrub tundras are present on the coarser-textured ancient beach ridges (Lindsey 1952).

Turning south, the southern limit of upland tundra then crosses eastward over the Wopmay River near Wopmay Lake. Southeast of the Wopmay River, the southern limit of upland tundra passes east of Little Crapeau Lake, then crosses the Emile River SW of Rodrigues Lake, and continues SE crossing the north end of Indin Lake.

The upland tundra limit then parallels the south shore of Snare Lake, and turns SE passing about 10 km north of Gordon Lake. Upon approaching Great Slave Lake at McLeod Bay, the southern limit parallels the north shore, and lies about 150 m above the level of Great Slave Lake. Here the northward rise of the land creates a steep rise in cover of upland tundra north of Great Slave Lake. At the same time, rockland complicates the identification of valid upland tundra such that within 20 km of the north shore, the contour positions are somewhat approximate. The rapid gradient in vegetation change, however, constrains the contours to lie close to their true position. The necessary averaging of sample photos causes the southern limit to be "pushed" southward, but the contour lies within 5, or at most 10, km of its true position.

East of the mouth of the Lockhart River in the East Arm, Great

Slave Lake, the upland tundra limit drops SSE about 90 km, past the north end of Noman Lake (north of Nonacho Lake), and thence to the Taltson River. Paralleling the Taltson River for about 60 km, the limit then turns SE, then east, past Coventry Lake and continues to about midway of Wholdaia Lake. Forming a "V" northward in the valley of the Dubawnt, the upland tundra limit then turns SE past Atzinging Lake and thence to the south shore of Kasba Lake. Winding irregularly ESE past the south shore of Nueltin Lake, the upland tundra limit reaches the Seal River at about Stony Lake.

Crossing the Seal River at about Shethanei Lake, the southern limit passes 15-20 km north of North Knife Lake, and eastward into the Hudson Bay Lowlands. Upon reaching the Hudson Bay Lowlands this contour, dependent on the ratio of tree:upland tundra cover, loses reliability since both trees and upland tundra decrease dramatically in cover. In Figure 24B, the southern limit crosses the Churchill, but reference to Figure 13B shows that upland tundra is not found within the valley proper of the Churchill. East of the Churchill River, the southern limit of upland tundra winds erratically due more to the vagaries of available habitat than to climate.

Several southern outliers of the forest-tundra occur in the northwest and most of these have been described under section 4.3.6. In passing, these are: (a) NW of Aubry Lake, perhaps due to coarse-textured hummocky ground moraine; (b) SE of Lac Belot, where upland tundra reaches a cover of about 0.4% on isolated summits above 360 m, although photo quality is poor, and the contour is drawn slightly farther west than it should be; (c) due west of Smith Arm, Great Bear Lake, and SE of Lac à Jacques, a Cordillera outlier with a

maximum elevation of 840 m; (d) Grizzly Bear Mountain; (e) Norman Range.

Within the forest-tundra, hachured contours denote where tree cover falls to zero. Four such areas are plotted in Figure 24: (a) Caribou Hills, east of the Mackenzie Delta; (b) north of Hepburn Lake and south of the Coppermine River; (c) north of Snare Lake and south of Redrock Lake; (d) near the junction of the Hanbury and Thelon Rivers.

In the extreme southeast, the hachured contour approximates where tree cover falls to <1% due to almost complete dominance by treeless wetland. In this area, the tree:upland tundra ratio falls below 1000.

4.3.17.4 Relative locations of steep vegetation change

Across much of the western region, steep vegetation gradients occur near the northern limit of the forest-tundra. North of Great Slave Lake, sharp vegetation gradients shift from the northern to the southern half of the forest-tundra and retain this location eastward to Hudson Bay.

Between the extreme geographic limits of tree and upland tundra communities, these two vegetation types vie for areal dominance of the forest-tundra. With the exceptions of the extensive wetlands of the Mackenzie Delta and the Hudson Bay Lowlands, the ratio of tree:upland tundra cover provides a measure of relative dominance.

Because the ratio has been $\log_{10}$ transformed, each contour represents a 10-fold change in ratio relative to its neighbor.

When the position of the narrow 1:1 ratio line in Figure 24B.1 is considered relative to the north and south limits, a few general trends appear. In the western half of the study region (west of Yellowknife), the relative positions of the contours vary greatly. Across much of the western region, the 1:1 contour lies closer to the northern than to the southern limit of the forest-tundra, indicative of high tree cover well to the north, then a rapid fall to zero trees. This is most true (a) east of Sitidgi Lake to east of the Kugaluk River; (b) between the middle and upper reaches of the Anderson and Horton Rivers SE to Dease Arm (GBL); (c) eastward from McTavish Arm (GBL) to Point Lake. The erratic changes in the relative positions of the north, 1:1, and south lines in the west are understandable in light of the major discontinuities in elevation, parent material, and perhaps the influence of fire history (e.g., east of Inuvik).

On an ENE axis running from the middle Wopmay River to western Point Lake, relative dominance of tree and upland tundra vegetation undergoes a dramatic change. Northwest of this axis, most vegetation change takes place in the northern half of the forest-tundra. Southeast of this axis tree cover falls rapidly (upland tundra increases rapidly) in the southern half of the forest-tundra, then extends well to the northward in a dominantly tundra landscape. This pattern is remarkably uniform and striking in northern Manitoba--southern Keewatin.

In Figure 24B.2, the full range of seven contours is depicted. At

this minimum of averaging (4 neighbors), local and regional variations in the dominance of forest-tundra vegetation are evident. The overall generalized positions of the contours and the rates of change they depict are presumably most closely correlated with climate. Local and regional variations in climate, parent material and drainage, depth to bedrock, and history manifest themselves in the local variability of the contours of vegetation cover. Each of the contours may be interpreted as a "treeline". It should be noted that extensive fieldwork provided no evidence to support the notion of distinct treelines of sexually and asexually reproducing trees. Sexual reproduction occurs up to the limit of trees as a species. The prevalence of sexual reproduction simply decreases northward in favor of asexual reproduction. To demarcate separate zones would be to engage in an unverifiable exercise that would mislead rather than clarify.

4.3.18 Smoothed depictions of upland tundra and tree cover

Gradients of smoothed upland tundra and tree cover are described by a sigmoid curve. In the southeast, most vegetation takes place in the southern half of the forest-tundra; in the northwest, steep gradients are often located near tree limit. Both tree and upland tundra cover are depressed in the Hudson Bay Lowlands.

Heavy averaging of the tree and upland tundra cover data (12 neighbors), greatly dampens local variability, and does not permit

depiction of the zero contour. The bold line in both Figures 14B and 25B is the 5% contour. In these plots it is the relative position of the contours and the gradients they depict that is relevant. Local accuracy is lost in the averaging.

The generalized slope of percent cover of upland tundra (Figure 14A) describes a sigmoid curve truncated at its lower end. In some localities near the central meridian, e.g., near the East Arm of Great Slave Lake, cover decreases so abruptly as to describe a parabola. From the Kugaluk River westward to the Mackenzie Delta, percent cover of upland tundra increases steadily northward and usually does not reach a plateau. The Mackenzie River forms a trough in upland tundra cover; west of the Mackenzie, percent cover rises all along the Cordillera, but again does not reach a plateau.

Smoothed cover of upland tundra rises northward from 5 to 50% in 45-90 km across the entire subarctic study region. West of the Horton River, the 80% level is rarely reached. From the Horton east to the Thelon, cover rises from 50 to 80% in 18-60 km. Eastward from the Thelon, the rise from 50 to 80% cover may take as little as 45 km near Mueltin Lake or as much as 290 km through Manitoba--Keewatin. The Hudson Bay Lowlands sharply depress potential upland tundra cover by their scarcity of upland habitats.

Figures 25A and B present smoothed depictions of tree plus recently-burned cover. The curve of the gradient in Figure 25A is truncated sigmoid. South of the east end of the Eskimo Lakes, the curve is steep and abrupt enough to describe a parabola. The irregularity of the surface in the Great Bear Lake region is due

primarily to highlands. The more gradual slope in the east is evident, as is high tree cover in the Thelon, Dubawnt, and Kazan valleys, and farther east, the Henik Lakes. Note the depressing effect on tree cover of the Hudson Bay Lowlands. In general, trees reach their highest cover in the eastern subarctic.

West of the Thelon, smoothed tree cover falls from 50 to 5% in 35-70 km. East of the Thelon, the same fall in tree cover may require 60-240 km. Across the subarctic, the fall from 80 to 50% cover usually takes place within 40 km. The major exceptions are east of the Mackenzie and east of McTavish Arm, Great Bear Lake; in these areas, the 80 to 50% decline may take as much as 70-110 km.

Figures 14 and 25 may be summarized: (a) in the southeast, tree and upland tundra cover change most rapidly in the southern portion of the forest-tundra, with gradual change to the north; (b) from the Mackenzie eastward to the Coppermine River, vegetation changes tend to be more rapid at the northern limit of the forest-tundra, and gradual at its southern limit; (c) north of Great Slave Lake, steep vegetation gradients cross over from the northern forest-tundra to the southern forest-tundra. This crossover can be seen on a line extending NNE from the Wopmay River to Point Lake. Gradients of vegetation change in relation to climate are considered in section 5.2.

4.4 Soil pH, cation exchange capacity, and nitrogen and potassium levels in the study region

Typical soils in the northwest are loamy textured, have slightly higher pH's and much greater CEC's than the sandy loams and loamy sands of the Shield. Some Shield soils, however, are basic in pH. Nitrogen and potassium levels average about 3-10 times higher for the northwest than for the Shield.

Soil and vegetation studies have been conducted over much of the study region; Appendix 3 provides a selection of representative vegetation and soils data. Although differences in approach and the sparsity of data militate against a comprehensive treatment, a general review of available soil nutrient data may aid in understanding the forest-tundra environment. Soil acidity and cation exchange capacity provide a general indication of the nutrients available to plants (Zoltai and Johnson 1978); these and nitrogen and potassium data are summarized in Tables 2 and 3.

Quantitative comparisons of pH and cation exchange capacity may be subject to errors, as both pH and CEC are somewhat method-dependent (Black 1968; Kohnke 1968; e.g., Losey et al. 1973), and thus statistical tests for differences should be viewed conservatively.

Acidic and basic parent materials, and also coarse- and

fine-textured soils, are extensive both in the northwest and on the Shield. As such, the comparisons of pH and CEC apply to average conditions. In order for regional differences to be evident, therefore, fine-textured Shield soils have been separated from the much more typical coarser-textured Shield soils (see Table 2 footnotes).

Organic horizons of the Shield average more acidic than those of the northwest (Table 2), but the difference is only weakly significant. A horizons of the Shield (for soils of sandy loam texture or coarser) are significantly more acidic than those of the northwest, but B horizons are essentially identical in pH in the soils examined. C horizons of the Shield average somewhat more acidic than those of the northwest, but again the difference is non-significant at $p=0.05$. There is a wide range in pH values for all horizons in both the northwest and the Shield.

The "typical" Shield soil overlies acidic crystalline rocks, is sandy loam or loamy sand textured, and is derived from a till layer 2-8 m thick. Shield soils, however, are more diverse in parent materials than those of the northwest. Many soils are derived from Archean sediments, metasediments, volcanics (usually basic), and Proterozoic sandstones (Geological Survey Canada 1968). Glaciolacustrine and glaciomarine modification adds further diversity to Shield soils (Geological Survey Canada 1967). Soils data are still too fragmentary to differentiate these soils from those of "typical" Shield terrain.

Table 2. Summary of soil pH and cation exchange capacity for the study region. "Northwest" includes the Arctic Coastal Plain, Interior Plains, and two Cordillera soils. Data are summarized from the sources listed in Appendix 3. The Shield data are for soils of sandy loam texture or coarser; see footnotes # and *. The test for difference between Northwest and Shield soils is a Mann-Whitney probability of non-significance.

Soil pH

Hor.	Northwest				Shield				Test
	Median	Range	N	S.D.	Median	Range	N	S.D.	Prob.
org.	4.7	(3.4-8.0)	19	1.4	3.8	(3.0-7.8)	19	1.3	0.077
A	5.3	(3.6-8.0)	11	1.5	3.9	(3.0-5.5)	21	0.7	0.011
B	5.0	(3.7-8.0)	20	1.3	5.3	(3.6-7.4)	39	0.8	0.259
C	6.2	(3.6-8.0)	30	1.4	5.0	(3.9-7.3)	33	1.0 #	0.102

Cation exchange capacity (meq/100g)

org.	71.0 (17.6-127.)	7	34.8	94.2 (49.1-155.)	14	41.6	0.048
A	26.8 (4.9-33.1)	9	9.6	6.2 (1.5-51.5)	14	12.8	0.005
B	18.6 (5.0-25.2)	17	6.7	3.4 (1.6-11.9)	20	2.8	0.0001>p
C	20.9 (1.0-38.2)	21	10.4	1.5 (0.3-2.5)	29	0.6*	0.0001>p

pH of Shield soils finer than sandy loam in texture is higher: C horizon median pH 7.8, range 5.0-8.4, N=18, +/- 0.9 for soils of the Coppermine River, Dismal Lakes, and East Arm of Great Slave Lake.
 * cation exchange capacity of three fine-textured Shield soils: median 19.4, range 2.5-22.6, N=3, +/- 10.8

For example, in Shield soils of texture finer than sandy loam, C horizon pH is generally high (median 7.8 for soils of the Coppermine River, Dismal Lakes, and the East Arm of Great Slave Lake; Table 2). Perhaps the most basic soils of the Shield are silt loams of the lower Coppermine River and Dismal Lakes. The bedrock of this area is variable, and includes limestone, dolomite, granitic rocks, syenite, gabbro, diabase dykes, conglomerate, sandstone, metagreywacke, and interbedded red shales and dolomites (Geological Survey Canada 1968; field observ.).

West of the Shield, on the Interior Plains and the Arctic Coastal Plain, till-derived soils have developed over carbonate rocks, sandstone, shale, mudstone, and siltstone. Soil acidities for the region range widely between 3.6 and 8. Highest pH's (7-8) are found on calcareous terrain such as along the upper Horton River; non-calcareous tills generally have pH's between 5-6. Lowest pH's (<4) are found on non-calcareous colluvium in the unglaciated mountains of the Cordillera (Zoltai and Pettapiece 1974).

Soils derived from carbonate tills along the Horton River typically have textures of loam, silt loam, or silty clay loam, and pH's in the C horizon of 8.0 (Zoltai et al. 1979; this study). Much of the land between the Horton and Anderson Rivers is underlain by Devonian shale, limestone, sandstone, and Cretaceous siltstone, mudstone, and shale. The typical till is clay to clay loam textured, and sparsely stony in the south (Anderson River Morainic Plains of Zoltai et al. 1979). In the north (Smoking Hills Uplands), till is patchy; most surficial material is clay

textured and colluvial or aeolian-like (Zoltai et al. 1979). Regional pH in the Smoking Hills of the Horton River exceeds 7.5 (Havas and Hutchinson 1983).

Glaciofluvial, alluvial, and ice-contact derived soils studied along the Horton River had pH's between 7.0 and 8.0, and textures ranging from sand to silty clay loam (see Appendix 3).

The median cation exchange capacity for organic soils on the Shield is significantly higher than that of the northwest (Table 2), but most of this capacity is taken up by hydrogen ions (Appendix 3). Mineral horizons of the northwest show CEC's 4-14 times greater than those of coarser-textured Shield soils (Table 3). Due to enrichment with organic matter, A horizons have the highest CEC's. Cation exchange capacity of northwest B horizons is 5.5 times greater, and that of C horizons is 14 times greater than those of the Shield. Although there are insufficient data, fine-textured Shield soils probably have CEC's similar to those of the northwest (median 19.4, range 2.5-22.6, N=3, +/- 10.8, for C horizons).

Total nitrogen levels peak in organic horizons, showing a median of 1.70% for Shield organic soils, and 0.07% for Shield A horizons (insufficient data for northwest organic soils and A horizons). Although nitrogen data are also scant for B and C horizons, of the soils available, percent total nitrogen averages about 3-10 times greater for northwest than for Shield soils (Table 3).

Table 3. Summary of nitrogen and potassium levels for soils* of the study region. "Northwest" includes the Arctic Coastal Plain, Interior Plains, and two Cordillera soils. By inspection of data, "trace" was arbitrarily defined as 0.04 for both N and K values. Due to the varied sources of data, and the necessary approximations of "trace", no statistical tests are given. Data for BC horizons were tabulated under C horizons. Values for the Shield are for soils of sandy loam texture or coarser. "-----" denotes insufficient data.

Total Soil Nitrogen (percent)						
Horizon	Northwest			Shield		
	Median	Range	N	Median	Range	N
organic	-----	-----	--	1.70 (0.40-2.69)		14
A	-----	-----	--	0.07 (0.02-0.50)		15
B	0.11	(0.05-0.18)	4	0.04 (0.003-0.10)		19 **
C	0.13	(0.01-0.31)	5	0.01 (0.00-0.04)		13 **
Soil Potassium (meq/100g)						
organic	0.97	(0.36-4.10)	7	0.30 (0.10-3.10)		14
A	0.51	(0.12-1.00)	10	0.07 (0.03-0.40)		14 **
B	0.22	(0.12-0.44)	12	0.04 (0.03-0.14)		20 **
C	0.29	(0.02-0.70)	15	0.04 (0.03-0.12)		30 **

* Data are summarized from Losey et al. (1973); Tarnocai (1973); Zoltai and Tarnocai (1974); Pawluk and Brewer (1975); Zoltai and Johnson (1978); and Bradley et al. (1982).

** exclusive of lacustrine clay Redcliff Island soil association in the East Arm of Great Slave Lake; Redcliff % N = 0.1 in both B and C horizons, and K meq/100g = 0.2 in A, 0.6 in B, and 0.7 in C horizons (cf. Bradley et al. 1982)

Soil potassium levels are higher for soils of the northwest (Table 3). Organic horizons of the northwest showed three times as much, and A horizons seven times as much potassium as those of the Shield. For B and C horizons, K levels in the northwest averaged 5-7 times greater than those of the typical coarse-textured soils of the Shield.

By virtue of their slightly higher pH and much greater CEC, nitrogen, and potassium levels, average northwest soils provide a more nutrient-rich growing medium than do typical Shield soils. The richest soils of the forest-tundra are probably loams on calcareous parent materials, e.g., in the Coppermine--Dismal Lakes region, and the southern portion of the Horton and Anderson Plains. Vegetation and soil relationships are described in sections 4.5 and 4.6, and discussed in 5.2.4.

4.5 Plant species indicating soil pH, moisture, and bioclimate in the study region

Substrate preference and geographic distribution of forest-tundra species are summarized as a basis for terrain interpretation and vegetation classification. A break in species occurrence takes place near the Shield/sedimentary terrain boundary north of Great Slave Lake which coincides with both a marked change in the orientation of vegetation contours and in the latitude of the forest-tundra.

Habitat preferences of arctic and subarctic plants are somewhat dependent upon the region (Griggs 1934). For example, *Ptilidium ciliare* is evidently an acidophile in Minnesota and adjacent regions (Schuster 1977), but is usually found on calcareous soil and humus in Alaska (Steere and Inoue 1978). Dwarf birch, a species of bogs and wet mountain slopes and summits at its southern limit (Gleason and Cronquist 1963), shows little pH or moisture preference in the high subarctic. Black spruce, a species of *Sphagnum* bogs at its southern limit (Gleason and Cronquist 1963), grows in wet to dry soils, organic and mineral, and over bedrock in the subarctic and much of the boreal region. White spruce, normally a mesophyte, prefers wet to wet-mesic soils at its northern limit. Thus, indicator species must be interpreted in a regional context.

A summary of forest-tundra indicators of soil pH, soil moisture, and bioclimate is offered as a framework for landscape interpretation and vegetation classification (Tables 4A-D). Data are primarily from fieldwork and ordinations, supplemented by regional studies listed in Figure 2. Indicators have been compared to species accounts in Steere (1978), Steere and Inoue (1978), Porsild and Cody (1980), and Thomson (1984):

Table 4A. Plant indicators of soil pH and moisture in the forest-tundra of the NWT.*

ACIDIC	BASIC
HYDRIC	
<i>Carex saxatilis</i>	<i>Calliergon giganteum</i>
<i>Drepanocladus fluitans</i>	<i>Carex garberi</i>
<i>Drosera rotundifolia</i>	<i>C. gynocrates</i>
<i>Kalmia polifolia</i>	<i>C. physocarpa</i>
<i>Lophozia binsteadii</i>	<i>Catoscopium nigrum</i>
<i>Oxycoccus microcarpus</i>	<i>Drepanocladus badius</i>
<i>Pinguicula villosa</i>	<i>Eriophorum callitrix</i>
<i>Polytrichum commune</i>	<i>Meesia triquetra</i>
<i>Sphagnum balticum</i>	<i>Oxytropis deflexa</i>
<i>S. fuscum</i>	<i>Pedicularis sudetica</i>
<i>S. russowii</i>	<i>Scorpidium scorpioides</i>
MESIC	
<i>Arctostaphylos alpina</i>	<i>Arctostaphylos rubra</i>
<i>Betula papyrifera</i>	<i>Carex concinna</i>
<i>Cladonia crispata</i>	<i>C. scirpoidea</i>
<i>Equisetum sylvaticum</i>	<i>Distichium capillaceum</i>
<i>Geocaulon lividum</i>	<i>Hedysarum alpinum</i>
<i>Gymnocolea inflata</i>	<i>Hypnum bambergeri</i>
<i>Pedicularis labradorica</i>	<i>Isopterygium pulchellum</i>
<i>Peltigera malacea</i>	<i>Lupinus arcticus</i>
<i>Pleurozium schreberi</i>	<i>Oncophorus wahlenbergii</i>
<i>Ptilium crista-castrensis</i>	<i>Oxytropis maydelliana</i>
	<i>Potentilla fruticosa</i>
	<i>Salix reticulata</i>
XERIC	
<i>Agrostis borealis</i>	<i>Bryum wrightii</i>
<i>Carex deflexa</i>	<i>Carex glacialis</i>
<i>C. supina</i>	<i>C. nardina</i>
<i>Cryptogramma crispa</i>	<i>C. rupestris</i>
<i>Diapensia lapponica</i>	<i>Cetraria tilesii</i>
<i>Dryopteris fragrans</i>	<i>Chrysanthemum integrifolium</i>
<i>Hierochloa alpina</i>	<i>Dactylina ramulosa</i>
<i>Loiseleuria procumbens</i>	<i>Erigeron compositus</i>
<i>Sphaerophorus globosus</i>	<i>Kobresia myosuroides</i>
<i>Stereocaulon paschale</i>	<i>Oxytropis hyperborea</i>
<i>Xanthoparmelia centrifuga</i>	<i>Physconia muscigena</i>
(saxicolous, sometimes on soil)	<i>Salix niphoclada</i>
	<i>Tortula ruralis</i>

* The acidic--basic division is taken as pH 7. Hydric refers to soil conditions from submerged to poorly-drained; mesic to imperfectly- to well-drained; and xeric to rapidly- to excessively-drained and often exposed conditions. No distinction is made between mineral and organic soils.

While the dual soil moisture and pH indicators in Table 4A are informative and useful in vegetation classification (e.g., *Arctostaphylos alpina*, *A. rubra*, *Carex concinna*), many of these species are inconspicuous (e.g., *Isopterygium pulchellum*, *Lophozia binsteadii*). In contrast, some species, many of which are dominant on the Shield and of relatively minor importance elsewhere, are poor indicators of pH and moisture conditions: *Betula glandulosa*, *Empetrum nigrum*, *Ledum decumbens*, *L. groenlandicum*, *Salix arbusculoides*, *S. glauca*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Dicranum acutifolium*, *Cetraria cucullata*, *C. islandica*, *C. nivalis*, *Cladonia mitis*, and *C. rangiferina*.

Important species which indicate only pH are *Carex bigelowii*, *Picea mariana*, and *Ptilidium ciliare* (acid); *Picea glauca* (circumneutral to basic); and *Carex vaginata*, *Dryas integrifolia*, *Aulacomnium acuminatum*, and *Ditrichum flexicaule* (basic).

Indicators of moisture only are *Arctophila fulva*, *Carex aquatilis*, *Eriophorum angustifolium*, and *Salix alaxensis* (wet); *Arctagrostis latifolia*, *Eriophorum vaginatum*, *Salix planifolia*, *Aulacomnium palustre*, *Drepanocladus uncinatus*, *Hylocomium splendens*, *Rhytidium rugosum*, *Tomenthypnum nitens*, *Cetraria andrejevii*, *C. laevigata*, and *Cladonia gracilis* (broadly mesic); and *Polytrichum piliferum* (dry). *Cassiope tetragona* indicates wet-mesic to mesic conditions and may be somewhat calciphilic.

In addition to the two major gradients of moisture and pH, a

third, climatic gradient is evident. As the forest-tundra is both a distinctive vegetation and climatic transition, indicators are numerous, and only a sampling of conspicuous species is given below (Tables 4B, 4C, 4D). For comparison, see Bradley et al. (1982) for plant indicators of bioclimate in the Lockhart River map area, and Ahti (1978) for arctic--subarctic indicators in northern Europe.

The most obvious bioclimatic indicators are the trees. Tree-size balsam poplar and aspen reach their northern limits in the high boreal region; jack pine reaches its northern limit near the high boreal--low subarctic transition; and paper birch reaches its limit in the southern half of the high subarctic; larch, white spruce and black spruce extend through the high subarctic.

Table 4B. Conspicuous species extending northward into the low subarctic (extending rarely or sporadically into the high subarctic)*.

<i>Arctostaphylos uva-ursi</i> **	<i>Pleurozium schreberi</i>
<i>Equisetum sylvaticum</i>	<i>Ribes triste</i>
<i>Geocaulon lividum</i>	<i>Rosa acicularis</i> **
<i>Juniperis communis</i> **	<i>Rubus acaulis</i>
<i>J. horizontalis</i>	<i>R. strigosus</i>
<i>Myrica gale</i>	<i>Viburnum edule</i>
<i>Pinus banksiana</i>	

* *Stereocaulon paschale* and *Cladonia multiformis* extend north through the high subarctic, but are less abundant than in the low subarctic.

** May be common in the forest-tundra of the far northwest (see Ritchie 1984).

Table 4C. Conspicuous species extending northward into the high subarctic or low arctic.

<i>Alnus crispa</i>	<i>C. deflexa</i>
<i>Betula occidentalis</i>	<i>Cladonia crispata</i>
<i>B. papyrifera</i>	<i>Ptilidium ciliare</i>
<i>Carex aquatilis</i> var. <i>aquatilis</i>	<i>Ptilium crista-castrensis</i>
<i>C. capitata</i>	<i>Salix planifolia</i>
<i>C. concinna</i>	

Table 4D. Conspicuous species extending southward into the low arctic, high subarctic, or northern Rocky Mountains*.

<i>Alectoria ochroleuca</i>	<i>Lesquerella arctica</i>
<i>Alopecurus alpinus</i>	<i>Luzula nivalis</i>
<i>Androsace chamaejasme</i>	<i>L. wahlenbergii</i>
<i>Arctagrostis latifolia</i>	<i>Salix arctica</i>
<i>Arctophila fulva</i>	<i>Masonhalea richardsonii</i>
<i>Campanula uniflora</i>	<i>Oxyria digyna</i>
<i>Carex aquatilis</i> var. <i>stans</i>	<i>Oxytropis arctobia</i>
<i>C. membranacea</i>	<i>Papaver radiculatum</i>
<i>C. rariflora</i>	<i>Parrya arctica</i>
<i>C. rupestris</i>	<i>Phyllodoce coerulea</i>
<i>Cassiope tetragona</i>	<i>Salix arctophila</i>
<i>Chrysanthemum integrifolium</i>	<i>S. herbacea</i>
<i>Cinclidium arcticum</i>	<i>S. lanata</i>
<i>Cornicularia divergens</i>	<i>S. niphoclada</i>
<i>Dactylina arctica</i>	<i>S. reticulata</i>
<i>Diapensia lapponica</i>	<i>Saussurea angustifolia</i>
<i>Dicranum amannii</i>	<i>Saxifraga oppositifolia</i>
<i>D. angustum</i>	<i>Thamnia subuliformis</i>
<i>Hierochloa alpina</i>	

* *Betula glandulosa* and *Salix glauca*, though wide-ranging, reach their greatest prominence in the high subarctic. *Dryas integrifolia* reaches its greatest dominance in the low arctic, but extends southward into the high subarctic as a dominant species on calcareous terrain.

Classification of common forest-tundra species by their stand occurrences (Table 4E) indicates four geographically-correlated groups. The upper (southeast) group (33 species, 22% of total) is characteristic of the Shield, low to high subarctic, and/or acidic coarse-textured soils (e.g., in decreasing strength of preference, *Salix planifolia*, *Carex bigelowii*, *Picea mariana*, *Stereocaulon paschale*, *Betula papyrifera*, *Alnus crispa*, *Pleurozium schreberi*, and *Arctostaphylos alpina*).

Widespread species, many of which are dominant on the Shield and of relatively minor importance elsewhere, comprise the second group (e.g., *Vaccinium vitis-idaea*, *Ledum groenlandicum*, *L. decumbens*, *Empetrum nigrum*, *Cladonia mitis*, *Vaccinium uliginosum*, and *Betula glandulosa*; 32 species, 22%). In comparison, widespread species showing a greater occurrence in the northwest are characterized by *Picea glauca*, *Carex glacialis*, and *Rhytidium rugosum* (23 species, 16%).

Species characteristic of the fine-textured loams of the northwest, high subarctic to low arctic, and/or basic often moist soils comprise the northwestern group (69 species, 41%). In increasing strength of preference, some conspicuous members are: *Arctostaphylos rubra*, *Tomenthypnum nitens*, *Hedysarum alpinum*, *Bryum pseudotriquetrum*, *Dryas integrifolia*, *Ditrichum flexicaule*, *Salix reticulata*, *Potentilla fruticosa*, *Lupinus arcticus*, *Carex scirpoidea*, and *C. concinna*.

The discontinuity between the southeastern and northwestern species occurs near the Shield/sedimentary terrain boundary north of Great Slave Lake. Northwestern species are dominant on the

Shield (*sensu lato*) only in the Coppermine River region, where Archean sediments are overlain by fine-textured basic soils. An analagous discontinuity in species composition and abundance occurs at the Shield/Paleozoic boundary in the forests of the low boreal region in central Canada (LaRoi 1964). For example, LaRoi found that (1) *Abies balsamea* was the major associate in black spruce stands east of Lake Winnipeg; white spruce was the major associate westward. (2) Abundance of *Ledum groenlandicum* was greatest in black spruce stands east of Lake Winnipeg; where *Ledum* was not common (between Lake Winnipeg and the Rockies), *Rosa acicularis* was the usual dominant in the medium--low shrub stratum. (3) In white spruce--fir stands, the low tree--tall shrub layer was dominated by *Acer spicatum* in stands east of Lake Winnipeg; *Alnus crispa* was the usual dominant as far as Great Slave Lake, with *Salix* and/or *Salix/Alnus* dominating westward to Alaska.

The break in species occurrence and dominance in the forest-tundra, indicative of edaphic and geographic components in the vegetation, coincides with a marked change in the orientation of vegetation cover contours. At the Shield, the forest-tundra drops precipitously southward, both geographically and climatically (Figure 24). The prominence of arctic--alpine species in the northwest, and of low subarctic species in the southeast, highlights the disparate climates within the forest-tundra. Dominant plant communities are outlined in section 4.6; vegetation, climate, and terrain relationships are discussed in section 5.2.

Species	Study Areas							
	B	A	B	C	PT	SP	I	S S S I
(SOUTHEASTERN)								
Salix planifolia	++	+	++	++	+++	+	+	+
Rubus chamaemorus	++	+	+	++	++++	+	+	+
Luzula confusa	-	-	-	++	+++	+	+	+
Carex bigelowii	-	-	+	++	+++	+	+	+
Picea mariana	+++	+	+++	+++	+++	+	+	+
Stereocaulon paschale	++	+	+++	+++	+++	+	+	+
Cladonia crispata	++	+	+++	+++	+++	+	+	+
Larix laricina	+	+	+++	+	++	+	+	+
Geocaulon lividum	++	+++	++	+	++	+	+	+
Betula papyrifera	++++	+	+	+	+	+	+	+
B. occidentalis	+	+	+++	+	++	+	+	+
B. glandulosa	+	+	+++	+	++	+	+	+
Polytrichum piliferum	++	+	+++	+++	+++	+	+	+
Cetraria ericetorum	+++	+	+++	+	+++	+	+	+
Loiseleuria procumbens	+++	+	+++	+++	+++	+	+	+
Alnus crispa	+++	+	+	+	+++	+	+	+
Pleurozium schreberi	++	+	+++	+	++	+	+	+
Lophozia ventricosa	++	+	+	+	++++	++	+	+
Cladonia pleurota	+	+	+	+	++	+	+	+
C. deformis	++	+	+	+	++	+	+	+
Hierochloa alpina	++	+	+	+	+++	+	+	+
Calamagrostis lapponica	+	+	+	+	+++	+	+	+

10

[illegible]

4.6 Vegetation communities and associations of the forest-tundra

A greatly simplified and preliminary classification of forest-tundra vegetation is provided, with an emphasis on the vegetation of mesic mineral soils. Variations in physiognomy and species composition are noted along environmental gradients.

Preliminary results from ordinations of species and stands indicate two major gradients: soil pH and moisture. Figure 26 presents a stand ordination (DECORANA: Hill 1979a) based on presence of common vascular, bryophyte and lichen species. Supplementary data on vegetation associations, and soil pH and moisture, are provided in Appendix 5.

Stands in the lower left of the ordination are dry acidic, while those in the upper right are wet calcareous. Stands on acidic soils are clustered, indicating both greater stand similarity on the Shield and sampling bias toward mesic and dry-mesic sites in 1982 and 1983. In 1984, a broader range of moisture conditions was included in the sampling, including many wetlands. This coincided with a transition from coarse-textured acidic soils on the Shield to finer-textured basic soils in the northwest.

Stand position on the x-axis in Figure 26 is correlated both with pH ($r=0.740$, $p<<0.0001$) and moisture ($r=0.445$, $p<0.0001$). But soil pH and moisture are themselves correlated ($r=0.255$, $0.05>p>0.02$), probably because high pH soils tend to be

fine-textured. The y-axis is correlated significantly with moisture ($r=0.756$, $p<0.0001$), but not with pH.

In addition to soil pH and moisture, soil texture and climate also affect the species composition of stands. But due to the sharp landscape transition at the Shield/Northwest boundary, and the NW--SE orientation of the forest-tundra, variables such as pH, moisture, texture and latitude tend to be correlated, leading to complex gradients. Fine-textured soils were significantly wetter and higher in pH than coarse-textured soils ($r=0.376$, $p<0.01$; $r=0.509$, $p<0.001$, respectively). Because the finer-textured high pH soils of the northwest occur at higher latitudes than the Shield soils, latitude is also correlated significantly with texture ($r=0.672$, $p<0.0001$), pH ($r=0.605$, $p<0.0001$), and moisture ($r=0.332$, $p=0.001$). Strong correlations of site variables with latitude, and the effect of the climatic gradient by itself, resulted in a high correlation of latitude with stand position in the ordination. The correlation was greater along the x-axis ($r=0.794$, $p<0.0001$), than along the y-axis ($r=0.353$, $p<0.001$). Along this complex of interrelated environmental gradients, plant associations change continuously, making meaningful abstractions difficult to identify.

A second difficulty in identifying plant associations arises in comparing vegetation descriptions from various studies. Without a standard method for naming vegetation types and associations, it is sometimes difficult to determine whether differences or similarities in vegetation are real. A third difficulty is the paucity of published vegetation studies.

A fourth and perhaps most serious difficulty in vegetation classification derives from the ecology of the important species. Dominant plants such as *Empetrum nigrum*, *Vaccinium uliginosum*, and *V. vitis-idaea* can be found in hydric bogs, xeric stony terrain, and all habitats in between (Griggs 1934). These wide-ranging species may be dominant not only due to their broad ecological amplitudes, but also to the youth of the subarctic landscape, substrate instability, and to low competition (Hardy 1976). Griggs (1934:171) summarized:

"Lack of close-drawn competition... explains both the apparent lack of habitat preferences in the most characteristic species, and... the infinite variation in the composition of the plant cover."

Differences among forest-tundra plant communities are more reflected in changes of relative cover than in floristic composition (Hardy 1976). Thus the same factors which make the subarctic flora so simple-- youth of the landscape, short time since deglaciation, openness of the communities, and substrate instability-- make subarctic vegetation complex. The 'simplicity' of northern vegetation was given perspective by Drury (1956:101) when he wrote :

"...when it has been said that the vegetation of the North is less well organized or simpler, what has been meant is probably that it is made up of fewer species. It certainly is not simple."

Within the forest-tundra, it appears that soil moisture is the prime determinant of physiognomic vegetation types (e.g., lichen, graminoid, dwarf shrub, medium and tall shrub, tree); i.e.,

physiognomy is independent of soil pH. In contrast, plant associations are correlated with both pH and moisture.

Exclusive of azonal vegetation, forest-tundra vegetation communities on mesic mineral soils are divisible into four broad types (Table 4F, Figure 27): (A1) forest and forest-tundra on acidic soils; (A2) acidic shrub tundras; (B1) forest and forest-tundra on basic soils; (B2) basic shrub tundras. Shrub tundras are dominant northward and tree communities dominant southward. Forests of single-stemmed trees undergo a transition northward to woodlands, forest-tundras (widely-spaced, typically clonal spruce in a tundra matrix), and thickets in which clonal reproduction is prominent (Plates 5-8,11).

The black spruce/dwarf birch/ericad/lichen association dominates acidic loamy sand and sandy loam tills of the Shield in the southern portion of the forest-tundra (a similar black spruce/shrub/moss association dominates much of the low subarctic northwest on flat to gently sloping fine-grained acidic soils (Ritchie 1984); see footnote * Table 4F). Northward, dwarf birch--willow/ericad/lichen dominates mesic acidic soils.

On basic loamy soils of the northwest, forest and forest-tundra stands are dominated by the white spruce/dwarf birch--willow/*Dryas*--legumes/*Carex*/moss association (non-calcareous silt loams in the northwest support a white spruce/shrub/moss association (Ritchie 1984); see footnote ** Table 4F). Basic tundras support a diversity of plant associations, but the core type is the medium shrub/*Dryas*--legumes--*Arctostaphylos rubra*/*Carex*/lichen association on wet-mesic sites, with a

decline in medium shrubs on mesic and dry-mesic soils.

Variations in forest-tundra vegetation communities and associations are myriad along environmental gradients; some of these variations are alluded to in Table 4F and Figure 27. Vegetation communities of like moisture conditions are characterized by physiognomically similar vegetation, with various associations correlated with soil pH. For example, dwarf shrub/lichen tundras occupy dry exposed uplands and summits; on acidic soils, *Empetrum*--*Vaccinium vitis-idaea*/*Alectoria*--*Cornicularia* are typical; *Dryas*--*Carex*/*Cetraria*--*Ochrolechia* typify dry basic soils. On the wet mineral soils of slope bases and shallow depressions, *Eriophorum vaginatum* tussock tundras occur. In acidic tussock tundra, *Andromeda polifolia*, *Carex rotundata*, *Oxycoccus microcarpus*, *Rubus chamaemorus*, and *Sphagnum* spp. are typical. Tussock tundras on basic soil are indicated by *Carex scirpoidea*, *C. vaginata*, *Eriophorum callitrix*, *Campylium stellatum* and others. With poorer drainage, tussock tundras pass into *Eriophorum*--sedge meadows. Peat and permafrost aggradation and isolation from groundwater can lead to development of various bog types.

Table 4F. Overview of four major plant associations of mesic mineral terrain in the study region. "Ericad" as used here includes *Empetrum nigrum*. Emphasis is on common and conspicuous species. Data are from fieldwork, supplemented by studies cited in Figure 2 (see Table 4E, Figure 27).

(A) On mesic to dry-mesic, acidic mineral soils, often coarse-textured Shield tills

(A1) Forest to forest-tundra

black spruce/dwarf birch/ericad/lichen (see Plates 6,8)

ericads: *Arctostaphylos alpina*, *Empetrum*, *Ledum decumbens*,
L. groenlandicum, *Vaccinium uliginosum*, *V. vitis-idaea*

lichens: *Cladonia gracilis*, *C. mitis*, *C. rangiferina*,
C. uncialis, *Stereocaulon paschale*

associates: *Betula papyrifera*, *Carex bigelowii*, *Salix arbusculoides*, *S. glauca*, *Dicranum* spp., *Polytrichum juniperinum*, *Ptilidium ciliare*, *Cladonia amaurocrea*, *C. cornuta*,
C. crispata;

moister: *Alnus crispa*, *Equisetum scirpoides*, *Larix laricina*,
Oxycoccus microcarpus, *Rubus chamaemorus*, *Salix planifolia*,
Aulacomnium turgidum, *Hylocomium splendens*, *Sphagnum fuscum*,
S. recurvum; see (A2)

northern or drier: acidic tundra, see (A2)

on glaciofluvial sand: *Geocaulon lividum*, *Picea glauca*
Polytrichum piliferum

(A2) Tundra

dwarf birch--willow/ericad/lichen (see Plates 3,6,8)

willows: *Salix arbusculoides*, *S. glauca*

ericads: *Arctostaphylos alpina*, *Empetrum*, *Ledum decumbens*,
Loiseleuria procumbens, *Vaccinium uliginosum*, *V. vitis-idaea*

lichens: *Cetraria cucullata*, *C. nivalis*, *Stereocaulon paschale*,
Thamnolia subuliformis

associates: *Betula occidentalis*, *Carex bigelowii*, *Luzula confusa*, *Poa glauca*, *Saxifraga tricuspidata*, *Dicranum* spp.,
Polytrichum juniperinum, *P. piliferum*;

moister: *Andromeda polifolia*, *Carex aquatilis* var. *stans*,
C. rotundata, *Eriophorum vaginatum*, *Pedicularis labradorica*,
Pinguicula villosa, *Rubus chamaemorus*, *Salix arctophila*, *Scirpus caespitosus*, *Aulacomnium* spp., *Drepanocladus fluitans*,
Sphagnum

drier or more exposed: *Empetrum*--*Vaccinium vitis-idaea*/
Cornicularia--*Alectoris*; $\pm$ *Carex supina*, *Diapensia lapponica*,
Loiseleuria procumbens;

northern: *Cassiope tetragona*, *Dryas integrifolia*

Table 4F, continued--

(B) On mesic, basic soils, typically Northwest loamy tills**

(B1) Forest to forest-tundra

white spruce/dwarf birch--willow/*Dryas integrifolia*--
legumes/*Carex*/moss (Plates 1,5,7)

willows: *Salix glauca*, *S. lanata*

legumes: *Hedysarum alpinum*, *Lupinus arcticus*, *Oxytropis* spp.

Carices: *Carex capillaris*, *C. concinna*, *C. membranacea*, *C. misandra*, *C. scirpoidea*, *C. vaginata*

mosses: *Aulacomnium* spp., *Campylium stellatum*, *Distichium capillaceum*, *Drepanocladus uncinatus*, *Hypnum bambergeri*, *Hylocomium splendens*, *Rhytidium rugosum*, *Tomenthypnum nitens*

associates: *Anemone parviflora*, *Arctostaphylos rubra*, *Cardamine digitata*, *Cassiope tetragona*, *Ledum groenlandicum*, *Parnassia palustris*, *Potentilla fruticosa*, *Salix reticulata*, *Vaccinium uliginosum*;

moister: Carices and mosses increase in importance, see (B2)

northern or drier: basic tundra, see (B2)

(B2) Tundra

medium shrub/*Dryas*--legumes--*Arctostaphylos*/*Carex*/lichen
(Plates 1,4,5)

legumes: *Hedysarum alpinum*, *Lupinus arcticus*, *Oxytropis* spp.

Carices: *Carex membranacea*, *C. rupestris*, *C. scirpoidea*, *C. vaginata*

lichens: *Cetraria cucullata*, *C. nivalis*, *Ochrolechia upsalliensis*

associates: medium shrubs (*Betula glandulosa*, *Salix glauca*, *S. lanata*) may dominate on wet-mesic sites; *Potentilla fruticosa*, *Salix reticulata*, *Senecio atropurpureus*;

moister*: *Eriophorum vaginatum*, *Cardamine digitata*, *Carex atrofusca*, *C. lugens*, *C. scirpoidea*, *C. vaginata*, *Cassiope tetragona*, *Bryum pseudotriquetrum*, *Campylium stellatum*, *Distichium capillaceum*, *Drepanocladus revolvens*, *Hypnum bambergeri*

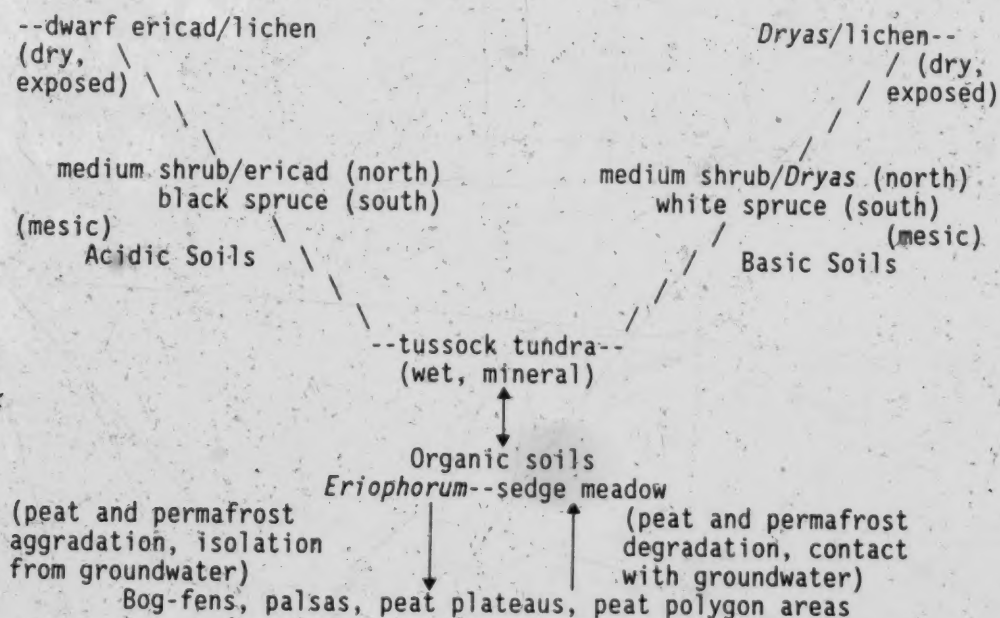
drier or more exposed: *Carex nardina*, *Salix niphoclada*, *Saxifraga oppositifolia*, *Cornicularia muricata* occur with *Dryas*/*Carex rupestris*/lichen; medium shrubs are absent

* On flat to gently sloping fine-grained glaciolacustrine deposits, loess, and tills with earth hummocks and little peat accumulation in the northwest, black spruce/shrub/moss open woodlands (Ritchie 1984) occur with a nearly identical species assemblage. In the northwest, this community is most widespread in the low subarctic.

Table 4F, continued--

- # With impeded drainage, dwarf birch, ericad, and willow cover is low, and *Eriophorum* tussocks are prominent in tussock tundras; with poorer drainage, tussock tundras pass into *Eriophorum*--sedge meadows; with peat accumulation and isolation from groundwater, bog types are formed.
- ** On non-calcareous silt loams in the northwest, a white spruce/shrub/moss association is common. Shrubs are *Alnus crispa*, *Betula glandulosa*, *Rosa acicularis*, *Salix glauca*, *Shepherdia canadensis*; mosses are *Aulacomnium turgidum*, *Dicranum elongatum*, *Hylocomium splendens*; associates: *Empetrum nigrum*, *Ledum decumbens*, *Ribes triste*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Viburnum edule*, *Peltigera aphthosa* (Ritchie 1984). Many of these species are more characteristic of the low subarctic, rather than high subarctic.

Figure 27. Forest-tundra vegetation and site relationships in the NWT, greatly simplified (see Table 4F).



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NOTICE

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IS HEAVILY DEPENDENT UPON THE
QUALITY OF THE THESIS SUBMITTED
FOR MICROFILMING.

UNFORTUNATELY THE COLOURED
ILLUSTRATIONS OF THIS THESIS
CAN ONLY YIELD DIFFERENT TONES
OF GREY.

AVIS

LA QUALITE DE CETTE MICROFICHE
DEPEND GRANDEMENT DE LA QUALITE DE LA
THESE SOUMISE AU MICROFILMAGE.

MALHEUREUSEMENT, LES DIFFERENTES
ILLUSTRATIONS EN COULEURS DE CETTE
THESE NE PEUVENT DONNER QUE DES
TEINTES DE GRIS.



Plate 1. South of Redrock Lake, white spruce tree cover begins to rise northward. In this view near Redrock and Rocknest Lakes, white spruce occurs in a willow--birch depression. Upland nets are outlined by medium shrub; light-toned tundra is probably dominated by *Dryas*--*Carex*--lichen. 114° 16' 30''W, 65° 29' 40''N; 21 June 84.



Plate 2. Well-developed patterned ground in lake shallows similar in form to that on uplands. 114° 20'W 64° 54' 20''N. 21 June 84.



Plate 3. Lichen rockland and dwarf ericad/lichen community. Cover dominants are saxicolous lichens such as *Asahinea*, *Hypogymnia*, *Lecidea*, *Parmelia*, *Rhizocarpon*, and *Xanthoparmelia*. Fruticose lichens and other plants, found primarily in rock cracks and depressions, are *Alectoria ochroleuca*, *Bryoria nitidula*, *Cetraria*, *Cladonia*, and *Cornicularia*; dwarf ericads, *Empetrum*, *Dicranum elongatum*, and *Polytrichum piliferum*. 111° 02' 35'' W, 64° 04' 15'' N; 17 June 84.

Plate 4. In this view of upland tundra on fine-textured basic soil, a diversity of moisture conditions is attested by dry to dry-mesic indicators *Carex rupestris* and *Salix niphoclada*, and mesic indicators *Arctostaphylos rubra*, *Hedysarum alpinum*, and *Lupinus arcticus*; other plants here are *Dryas integrifolia*, *Hedysarum alpinum*, *Oxytropis* spp., *Salix glauca*, and *S. lanata*. 125° 56' 15'' W, 69° 02' N. 20 Aug 84.





Plate 5. Forest-tundra landscape mosaic: white spruce forest and forest-tundra on south-facing slope; rich upland tundra associations dominated by willows (yellow-green), *Dryas*, *Carex*, and forbs; *Arctostaphylos rubra* (scarlet), dwarf birch and bilberry (orange, rusty green, dull red) are prominent; greyish semi-bare patches on north-facing slopes support *Artemisia frigida*. 125° 58'W, 69° 01' 40'N. 21 Aug 84.

Plate 6. Forest-tundra vegetation mosaic at the northern limit of trees in the Courageous Lake area. Black spruce clones occur in a *Salix planifolia*--*S. pulchra*--dwarf birch shrubland matrix with ericads--*Chamaedaphne/Equisetum*--*Pyrola/Sphagnum*--*Plagiomnium*--*Aulacomnium* and others. A brook runs through the stand. Foreground is dominated by dwarf birch--*Salix arbusculoides/Ledum decumbens*--*Empetrum*--ericads/*Cetraria*--*Cladonia*--*Alectoria*--*Cornicularia*, a widespread and important upland tundra association on the Shield. 111° 06'W, 64° 05' 30'N. 18 June 84.





Plate 7. In this white spruce clone excavated at the northern limit of trees, below-ground biomass greatly exceeds above-ground biomass. Note the reduction in stem diameter above winter snowpack level. The permafrost table rises from depths >1 m outside the clone to just below the large horizontal stems/roots inside the clone. $116^{\circ} 37' 40''$ W, $67^{\circ} 14' 55''$ N. 19 July 84.



Plate 8. Vegetation mosaic in the southeastern forest-tundra. Single-stemmed and clonal black spruce and white spruce on uplands and slopes; larch and tall shrubs on meadow and bog-fen margins; ericad/lichen tundra on summits and slopes. Upland in right mid-distance may have been burned over in the past. Near $106^{\circ} 29' 30''$ W, $61^{\circ} 56' 30''$ N. 29 Aug 83.



Plate 9. A poorly-drained gleysolic turbic cryosol (shock--
--sensitive) underlies a black spruce--larch/ericad--
Calamagrostis lapponica/*Sphagnum* grove on Barlow Lake.
103° 08' 20''W, 61° 54' 20''N. 5 Aug 83.



Plate 10. Soil in this dwarf birch/*Empetrum*--ericad/lichen
tundra, lying next to the tree grove soil shown in Plate 9, is a
well-drained brunisolic turbic cryosol. 103° 08' 20''W, 61° 54'
20''N. 5 Aug 83.

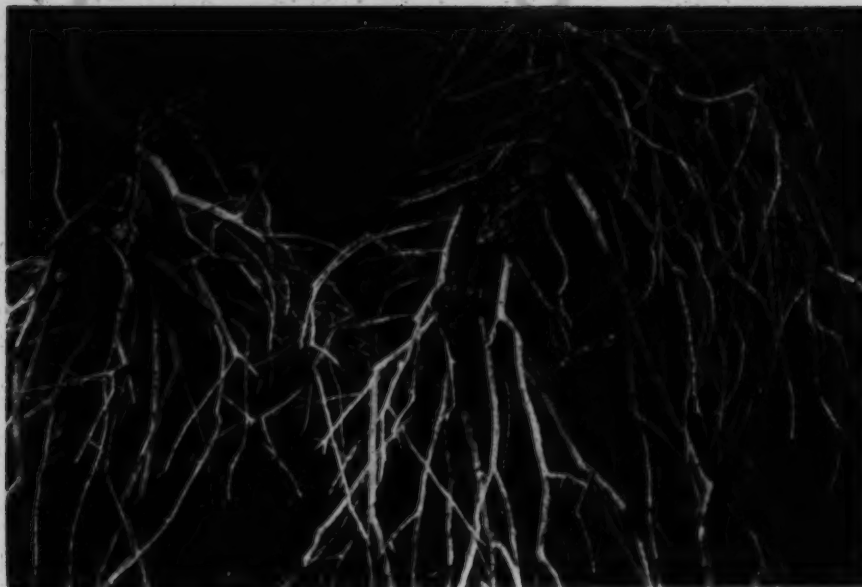


Plate 11. Both clonal and single-stemmed spruce may exhibit parabolic branches which curve abruptly downward, forming an interwoven tangle. Location: Thelon River between Warden's Grove and Hornby Point. Photo credit: Fred Vermuelen.



Plate 12. In this three year old burn in black spruce forest--tundra, no regeneration has yet occurred. *Ledum* and *Vaccinium* dominate shrub cover; dwarf birch is recovering by sprouts; lichen cover is 20% (much of it moribund) and moss cover is 9%; *Calamagrostis lapponica* is prominent. Regeneration from within the stand is unlikely, but unburned black spruce stands lie within 200 m. 113° 06' 45''W, 64° 15' 30''N. 13 July 82.

5 DISCUSSION

5.1 Relicts, treeline history, and the eastern forest-tundra

Although tree stands at their northern limits in the forest-tundra east of Great Slave Lake have been widely considered to be relictual (Bryson et al. 1965; Sorenson et al. 1971; Larsen 1974; Nichols 1976; Elliott-Fisk 1983; i.a.), northern forest-tundra "outliers" there lie climatically well south of most of the forest-tundra of the northwest (see Figure 24B.1). Those who adhere to the relict hypothesis regard the forest-tundra not as a zone but a line, with relict tree stands north of "treeline", "northern boreal forest border", etc. dating from warm periods, and relict tundra southward dating from cold periods (cf. Nichols 1976). The great breadth of the eastern forest-tundra is thus viewed as the result of the persistence, on a grand scale, of tree stands left behind by a southward retreating mid-Holocene forest. Such northern stands, seen as lacking the sanction of the present climate, may lack regular sexual reproduction.

There are two main difficulties with this view, stemming from (a) the problem of interpretation of paleoecological data; and (b) the question of what constitutes "relict" vegetation. Paleoecological data are considered below, followed by a consideration of relict status. An alternative edaphic and topoclimatic interpretation of forest-tundra vegetation is offered in sections 5.2.4.2 and 5.2.4.6.

5.1.1 Interpretation of forest-tundra paleoecological data

Difficulties in reconstructing past vegetation and climate are discussed. Evidence for Holocene treeline migrations is equivocal, difficult to generalize to regional status, and may be interpreted more parsimoniously in terms of climatically induced changes in pollen production, tree density, and consolidation of pre-existing stands.

Identification of a forest-tundra pollen spectrum in a continental region, crucial to understanding past movements of treeline, is difficult and requires supporting macro-fossil and other data (Lichti-Fedorovich and Ritchie 1968; Payette and Filion 1985). Ritchie (1977) identified three caveats in the use of pollen spectra for climatic and vegetation reconstructions: (1) A pollen sample may include only a small portion of the prevailing plant cover; many important taxa (e.g., lichens, ericads, *Dryas*) are "palynologically silent", a problem corroborated by Walker et al. (1981) for the Alaskan north slope, further exacerbated by high influx of exotic pollen. (2) Many of the older pollen assemblages have no modern equivalents. (3) Pollen influx values are likely more useful than pollen diagrams based on percentages.

A further consideration is the extrapolation of locally valid results to regional status. Oscillations of treeline observed in one locality may apply only to that area, as has been demonstrated by Kryuchkov (1970) for the forest-tundra of NE USSR. A comparison of July paleotemperatures in SW Keewatin, the East Arm, and the Coppermine River (Andrews and Nichols 1981) indicates significant variability

between regions, and in regional temperature trends. A scattering of dead spruce trees may have little paleoclimatic significance (cf. Nichols 1976:45).

Pollen, plant and insect macrofossils, and paleosols are the basis for the considerable volume of literature treating Holocene treeline migrations in "central Canada" (SW Keewatin). Unfortunately most of the fieldwork has been concentrated in one area extending from Kasba Lake north to Dimma Lake on the Kazan River, with much emphasis on Ennadai Lake (cf. Bryson et al. 1965; Nichols 1967a, b; Sorenson et al. 1971; Sorenson and Knox 1974; Sorenson 1977; Elliott-Fisk 1983; i.a.). Furthermore, Ritchie and Hare (1971) point out that Nichols's (1967a, b) conclusions rest upon tenuous assumptions regarding the importance of fluctuations in the frequency of *Sphagnum* spores, and that Nichols's interpretation of pollen frequencies is equivocal when compared to modern pollen assemblages from tundra, forest-tundra, and boreal forest in central Canada.

While changes in spruce pollen influx may indicate treeline movements, fluctuation in pollen production and/or tree density can result in similar changes in influx (Ritchie 1977) unaccompanied by shifts in treeline. It is possible that only small Holocene displacements took place in the forest-tundra between Great Slave Lake and Keewatin-Manitoba. Climatic changes may have been expressed primarily in changes in tree density and consolidation of pre-existing stands with negligible movements in vegetation zones, as appears to be the case for Tuktoyaktuk Peninsula (Ritchie and Hare 1971; Ritchie 1984), the Inuvik area (Ritchie 1977), for Churchill, Manitoba (Scott

et al. 1987a), and for northern Québec (Payette and Gagnon 1979; Morin and Payette 1984; Payette and Filion 1985).

Period of establishment of northern forest-tundra tree stands, inferred from paleobotanical and paleosol data on former extent of forest, is estimated as mid-Holocene (circa 6000-3500 BP: see Nichols 1976; Kay 1979). This estimate is based on the assumption that climate has been sufficiently unfavorable during the past 3500 yrs for establishment and expansion of stands in the northern forest-tundra. In a relative, but not an absolute, sense this may be true: the last 3000 yrs in the northern forest-tundra of Québec have been characterized by deforestation in excess of afforestation, brought about by climatic deterioration and fire, but unaccompanied by important movements of the forest-tundra boundaries (Payette and Gagnon 1985). Although some northern sites may have been treed more or less continually since the mid-Holocene, perhaps periodically disturbed by fire or minor climatic oscillations, such relict stands have never yet been identified. The oldest sites supporting clonal black spruce stands yet described, in the northern forest-tundra of Québec, are ~2000 yrs old, and the oldest black spruce and/or larch forests found to date are ~900 yrs old (Payette and Gagnon 1985).

Northern forest-tundra tree stands east of Great Slave Lake, if not mid-Holocene in origin or recently-established (since 1850: see following paragraph), may have originated during the period circa 1500-900 BP (~Little Climatic Optimum), when the "treeline" may have been located 50-100 km north of its present position (data from Sorenson and Knox 1974; Sorenson 1977). According to these data, at approximately 1000 BP, the "treeline" was located 100 km north; by 900

BP, 50 km north; and by 800 BP, 50 km south of its present location (thus "treeline" migrated a remarkable 150 km in 200 yrs, or 0.75 km/yr southward).

In the Kazan River area, the location of the "northern boreal forest border" is believed to have fluctuated over a latitudinal range of 250-330 km in the past 4000 yrs (Bryson et al. 1965; Bryson 1966; Sorenson and Knox 1974; Sorenson 1977). While tree establishment may have been successful in the period prior to 900 BP, it is debatable whether these and other treeline migrations postulated for Keewatin are valid (see Spear 1983; Bradley 1985:267; cf. Tikhomirov (1961) advocating a mid- to late Holocene forest limit in the USSR located 275-385 km north of its present limit; see also section 5.5). It is significant that, in contrast with major vegetation and climatic changes postulated for the Kazan River area, a paleoclimatic reconstruction undertaken on the Dubawnt River shows little change in either the extent or composition of tundra and forest since *circa* 3700 BP (Kay 1976, 1979).

Paleoecological interpretations requiring wide latitudinal shifts of the forest-tundra rest on the assumption that charcoal, macrofossil, and soil evidence indicate wholesale movements of the forest-tundra, as opposed to changes in vegetation cover within the forest-tundra (Payette and Gagnon 1985). While future research will shed light on the problem of Holocene treeline migrations in Keewatin, it is possible that many long-established tree stands in the northern forest-tundra there originated between 1500-900 BP, rather than in the mid-Holocene.

Paleosol and charcoal evidence for former movements of treeline must be interpreted cautiously. In light of the flammability of tundra types such as dwarf birch/ericad/lichen, dwarf ericad/lichen, and dwarf willow--birch (Wein 1976), the presence of charcoal in a tundra soil does not necessarily indicate the former presence of forest. Furthermore, podzols and brunisols exist in a continuum in nature; the boundary between the two soil types is arbitrary (Canada Soil Survey Committee 1978). Brunisols and brunisolic cryosols (arctic brown soils) are associated with forest-tundra and tundra vegetation, and podzols with boreal forest or heath vegetation. But these are rough approximations; e.g., soils with strongly leached Ae horizons and deeply stained B horizons have been observed under heath tundra in SE Mackenzie and southern Keewatin (Zoltai pers. comm.; field data), and brunisols are found under jack pine forests on sandy soils in central Alberta (cf. Fyles 1986).

Although paleopodzols and buried charcoal have been cited as evidence of Holocene treeline migrations in southern Keewatin (Bryson et al. 1965; Sorenson et al. 1971; i.a.), heath tundra fires and the brunisol--podzol continuum render climatic inferences difficult. Tree macrofossils and/or pollen are needed as corroborating evidence to infer former presence of forest as distinct from heath or forest-tundra (Payette and Gagnon 1979).

5.1.2 Relict vs. dynamic forest-tundra vegetation

Problems in regarding the northern forest-tundra as relictual are discussed. Examples of seed reproduction and newly-established trees at latitudinal and elevational limits are provided. Northern forest-tundra tree stands east of Great Slave Lake might be better viewed as in dynamic equilibrium with climate and characterized by episodic seed reproduction.

Perhaps much of the confusion in the North American literature on relict status stems from vague terminology. "Relict" connotes "a persistent remnant," something "left behind in a process of change," or "remaining after other parts have been removed or have disappeared" (Webster's Third New International Dictionary 1981). Specific to the forest-tundra, "relict" may connote any or all of the following: (1) disequilibrium with climate; (2) failure to reproduce sexually; (3) predominance of vegetative reproduction and multi-stemmed clonal growth forms ("krummholz", but cf. Holtmeir 1981); (4) clumps of typically black spruce growing north of the "treeline" or "forest border", restricted to "rare favorable sites" (see references listed in 5.1).

Another source of confusion may result from an expectation that forest-tundra vegetation dynamics should resemble those of the boreal forest. Yet forest-tundra tree stands commonly reproduce by a combination of cloning and seed reproduction; autogenic changes relating to soil temperature, moisture, and active layer are common; changes in tree vigor, growth form, and reproduction can be cyclic and/or opportunistic; seedling establishment is episodic, and thus

regeneration from seedling banks may be more typical than that from seed banks; fire return intervals generally exceed 200 years; and bioclimatic feedbacks are powerful (see Kryuchkov 1970, 1978; Hare and Ritchie 1972; Legere and Payette 1981; Bradley et al. 1982; Payette et al. 1982, 1985; this study). For example, succeeding white spruce forest-tundra and open crown forest near Churchill, Manitoba apparently show different rates and patterns of tree establishment and divergent trends in tree ring growth indices over time (Scott et al. 1987a).

A cornerstone of the relict school is the proposition that "regular sexual reproduction is absolutely necessary for long-term maintenance of northern tree stands" (Elliott-Fisk 1983:573). This statement is problematic in that time scales for "regular" sexual reproduction and "long-term" maintenance are undefined. Is seedling establishment 1 in 5 years, or even 1 in 30 years, sufficient to maintain a stand with a fire return interval of >300 years? No one knows. Even in the northern forest-tundra, the vast majority of tree stands (~95%) lie within 1-2 km of other trees (field and airphoto obsery.). If a stand is destroyed by fire or cutting, seeds produced outside the stand may colonize the area.

One must also question how long tree stands can regenerate themselves and persist and still be regarded as relicts. Certainly forest cover was more extensive during the mid-Holocene (~7000-3500 yr BP) and the Little Climatic Optimum (~1500-700 yr BP; see Kay 1979; Elliott-Fisk 1983, i.a.). But temperatures have been relatively cool for the 600 yrs prior to the 20th century, including the Little Ice Age (~1600-1850 AD). Thus northern tree stands have either: (1) established during a relatively warm time in the past circa 140

yr; (2) established during the relatively unfavorable 600 yr interval between the Little Climatic Optimum and the 20th century; or (3) persisted since the Little Climatic Optimum, or even the mid-Holocene. If (1) is true, can recently-established trees be regarded as relict?; if (2) is true, trees established during unfavorable times and are now relict during the relatively warm 20th century; if (3) is true, northern tree stands have reproduced sufficiently to maintain themselves in the face of 700-3500 yrs of low temperatures.

In contrast with the difficulty of documenting mid-Holocene forest stands, it is common to find relatively young clones and single-stemmed spruce stands in the northern forest-tundra of the Mackenzie District that have established since 1850 A.D. (e.g., Carey, Firedrake, Mary, and Mosquito Lakes, Horton River; this study). Similar young spruce have been observed at Dubawnt Lake; north of Dubawnt Lake near the junction of the Thelon and Dubawnt Rivers; and on the northwest shore of Aberdeen Lake (Hansell et al. 1971); and near Churchill, Manitoba (Scott et al. 1987a). In the Leaf River--Lake Minto region of northern Québec, larch seedling establishment was evidently vigorous between 1930-1970 (Payette and Gagnon 1979; Payette et al. 1982). Local altitudinal treelines in northern Québec have risen by a few tens of metres during the past 100 years, but the major recent vegetation changes there have been an increase in tree density and consolidation of pre-existing stands (Morin and Payette 1984; Payette and Filion 1985).

A 20th century northward extension of the Soviet forest-tundra has been noted by Tikhomirov (1961) and others. Elevations of subalpine timberlines have risen in most parts of the boreal USSR in this century

in response to recent climatic amelioration (Gorchakovsky and Shiyatov 1978), as has also been documented for the mountains of Fennoscandia and Alaska (Hustich 1979; Kullman 1979, 1986; Viereck 1979; Sonesson and Hoogesteger 1983; i.a.). Most of the Norway spruce (*Picea abies*) growing at tree limit in the southern Swedish Scandes established around the 1860's and the 1940's (Kullman 1986). Far from being relictual or historical, it appears that many northern and altitudinal tree outliers, in the NWT and elsewhere, are newly-established.

It is further problematic to generalize, from an apparent lack of seed reproduction in stands along the Kazan River, that treeline is in disequilibrium with climate in central Canada (cf. Elliott-Fisk 1983). Both sexual and asexual reproduction and expansion of tree stands have been observed west (Dubawnt River; this study) and east (Henik--Edehon Lakes; Zoltai pers. comm.) of the Kazan River. Recent studies in northern Québec indicate that the forest-tundra vegetation is in dynamic equilibrium with climate in the absence of other external disturbances, and that the opportunistic use of both sexual reproduction and cloning is an important asset in northern black spruce stands (Legere and Payette 1981; Payette et al. 1982, 1985).

Seedlings and saplings of black spruce, white spruce, and larch derived from parent trees with shrubby growth forms are less abundant than those from arborescent trees (Payette 1983). Yet both larch and black spruce in interior northern Québec show some seed regeneration up to their northern limits, although less than that in forest stands to the south (Payette et al. 1982). Black spruce clones there apparently

produce fewer seedlings than larch trees at their northern limits (Payette et al. 1982).

Both establishment and degeneration of tree stands may be viewed as normal forest-tundra and low subarctic processes, even in the absence of fire or climatic change, and may occur contiguous to one another (Drury 1956; Kryuchkov 1970, 1978); e.g., along the lower Horton River (field observ.). In the case of NE USSR, cycles between tree and tundra vegetation may be related to autogenic changes in insulating vegetation, soil temperature, snow depths, and thickness of the active layer. More documentation is needed regarding driving processes in both climatic and autogenic vegetation cycles.

The forest-tundra does not consist solely of a "treeline" in which tree and tundra vegetation undergo a steep transition. Rather this core of steep gradient lies "south" of a zone in which tundra dominates, and "north" of a dominantly forested landscape. The pattern of tree stands north, and tundra stands south of the steep transition is a fundamental characteristic of the forest-tundra, as typical as the treeline itself. Rather than invoke relict status for northern tree stands, study of present day landscape and vegetation may shed some light both on the past, and on this fundamental cover pattern (see 5.2.2, 5.2.3).

5.2 Vegetation, climate, and terrain relationships in the forest-tundra of the NWT

The distribution and areal cover of major vegetation components in the forest-tundra were detailed in the results section. This section begins with emergent general patterns-- what is normal or typical in the dominant vegetation of the forest-tundra-- and moves on to significant anomalies.

As a rough means of comparison, Table 5 summarizes relevant climatic and snow cover values for three longitudinal sectors of the forest-tundra. The accuracy of synoptic isopleths has been described in section 2.5 and the approximate nature of the climatic data must be borne in mind. It is, however, the climatic pattern which emerges that is important, not the absolute values. The vegetation--climate--snowcover patterns outlined below are the approximate bioclimatic limits within which forest-tundra vegetation functions. Note that the most climatically heterogeneous sector lies between Great Bear Lake and the Keewatin border.

Table 5. Summary of relevant climatic parameters for longitudinal sectors of the subarctic forest-tundra of the NWT.

"Northwest" extends from the Yukon border eastward to the east side of Great Bear Lake; "Central" extends from the east side of Great Bear Lake to the Keewatin border (exclusive of the central Thelon area); "Southeast" includes southern Keewatin and northern Manitoba. Values are rough approximations to be used for comparison. Climatic data are interpolated from Hare and Hay (1974) unless noted otherwise.

	<u>Northwest</u>	<u>Central</u>	<u>Southeast</u>
April Net Radiation (1y day^{-1})	15-35	30-70	35-75
Mean Annual Absorbed Solar Radiation (kly)	52-55	53-63	55-63
Mean Annual Net Radiation (kly)	12-18 (x-15)	15-24 (x-21)	15-25 (x-20)
July Mean Air Temp. @ Screen Level (C)	10 to 13	11 to 13	11 to 13
July Mean Air Temp. @ 850 mb Level (C)	4.5 to 6.5	4.5 to 7	6 to 7
Mean Annual Air Temp. @ Screen Level (C)*	-10.5 to -9	-10 to -6.5	-10 to -7
Mean Annual Heating Deg-Days (0 C base)			
N forest-tundra	3400-4100	2800-3500	3000-3600
S forest-tundra	2800-3400	2300-2800	2600
Frost-free Period (days)	50-65	55-80	70-75
Median Last Date of Winter Snow Cover > 2.5 cm	May 15-31	May 15-31	May 21-June 7
Mean Date of Rise of Mean Daily Air Temp. to 0 C	May 15-31	May 7-31	May 15-31
Mean Date of Fall of Mean Daily Air Temp. to 0 C	Sept 25	Oct 5	Oct 1

*Fletcher and Young 1978, and Hare and Hay by calculation

5.2.1 Location and orientation of the forest-tundra

The circumpolar forest-tundra corresponds broadly to zones of confluence of dominant air masses, and to relevant isorads and isotherms. In the subarctic NWT, relevant climatic and vegetation isolines show a clear NW--SE orientation. This orientation results from the interaction of the polar gradient in global solar radiation with the west to east weakening of Pacific air influence.

None would dispute the importance of climate as the primary correlate of the general position and orientation of vegetation formations (see Walter 1979; Woodward 1987). The circumpolar forest-tundra corresponds broadly to zones of confluence of dominant air masses, and to relevant isorads and isotherms. For example, in Eurasia (with the exception of mountainous eastern Siberia) the arctic front runs roughly west--east and the forest-tundra is oriented parallel to it (Lavrenko and Sochava 1954; Dolgin 1970; Krebs and Barry 1970; Lydolph 1977). In the NWT the summer arctic front is oriented NW--SE, slightly south of and parallel to the forest-tundra (Bryson 1966; Barry 1967). The arctic front determines the distribution of atmospheric water vapor and cloud cover in northern Canada and Alaska, and thus affects all components of the radiation balance (Hare and Ritchie 1972). In Labrador--Ungava the summer frontal pattern is broad and complex and likely derives from the conflict of air masses originating over Hudson Bay, North Atlantic, Pacific, and various arctic source regions (Bryson 1966; Krebs and Barry 1970). The corresponding

forest-tundra is broad and trends NE to Ungava Bay with decreasing frequency of cold Hudson Bay air, then SE with increasing frequency of cold north Atlantic air (Bryson 1966; Hustich 1966).

To what extent the location and orientation of the forest-tundra is the result of the summer airmass distribution (Bryson 1966), or the climatic patterns are themselves causally related to the structure of the natural vegetation (Hare and Ritchie 1972), is a fascinating and complex issue deserving of further research (see section 5.6).

Mountain ranges complicate the normally clear correlation between synoptic climate and forest-tundra, with the result that the forest-tundra of Alaska and eastern Siberia is areally complex (Dolgin 1970; Hare and Ritchie 1972). In Fennoscandia, mountain ranges, historical deforestation and afforestation, and fire further obscure the correlation between synoptic climate and the forest-tundra (Hustich 1966; Huovila 1970).

Relevant climatic (Hare and Hay 1974; Fletcher and Young 1978) and vegetation isolines (this study) in the subarctic NWT show a clear NW--SE orientation, a bioclimatic singularity which contrasts with the typical west--east orientation of vegetation and climatic zones in the circumpolar north. This orientation might be viewed as the result of the interaction of (a) the polar gradient in global solar radiation with (b) the west to east weakening of Pacific air influence (see Hare and Thomas 1979). Pacific airstreams moderate the spring climate first in the west and later extend inland as a wedge of warm, relatively moist air (Bryson 1966). Arctic air is supplanted from SW to NE. At a more basic

level, the oblique orientation of both vegetation and climatic isolines results from the north--south Cordilleran barrier to zonal flow (Ritchie, pers. comm.), which restricts Pacific air dominance in July to the southwestern Mackenzie District (see Bryson 1966: Figure 2).

The west to east march of spring is driven not only by proximity to Pacific source regions but also by the vegetation and snow cover. Low spring albedos of closed crown forest (0.1-0.3) contrast sharply with those of snow-covered tundra (0.7-0.8; Hare and Ritchie 1972). Deep, long-lying snow in northern Manitoba and southern Keewatin further slows the replacement of Arctic air by Pacific air.

At the synoptic level, the general position and orientation of the forest-tundra are clearly correlated with climate. Aside from irregular vegetation contours (Figures 9-24) which illustrate the complex response of vegetation to local climate, edaphic, fire, and historical factors, a major anomaly in the vegetation--climatic patterns remains. Upland tundra and tree cover gradients are oriented at a steeper NW--SE diagonal than critical thermal and radiation gradients (Figures 14, 24B.1, 25; cf. Hare and Hay 1974), indicating that the forest-tundra of the northwest receives less warmth and photosynthetic energy than the forest-tundra of central and southeast districts. On average, climatic and vegetation isolines cross one another somewhere between Great Bear and Great Slave Lakes. This topic and other examples of poor correlation with synoptic climate are taken up in section 5.2.4.

5.2.2 Width of the forest-tundra

While vegetation and climatic gradients correlate fairly well, synoptic climate cannot fully account for the great width of the forest-tundra in the southeast and the steep transition in many places elsewhere. Regional slope of the land probably accounts for much of the variation in the width of the forest-tundra.

As described in section 4.3.17, the subarctic forest-tundra of the NWT spans an average 150 ± 75 km and increases in width from northwest to southeast. This widening of the forest-tundra is most evident between the East Arm of Great Slave Lake and eastern Keewatin; greatest widths are encountered between the Dubawnt River and eastern Manitoba--Keewatin at 235-345 km.

Regional slope of the land probably accounts for much of the variation in the width of the forest-tundra. North of Dease Arm, Great Bear Lake, and in the central district from the Snare River SE to the East Arm of Great Slave Lake, elevations rise from south to north or SW to NE, parallel to the vegetation gradient. Evidently a strong topoclimatic gradient is created by the northward rise of elevation, eliciting steep vegetation gradients. Conversely, the NE fall of elevation between the East Arm and eastern Keewatin--Manitoba is likely instrumental in helping to account for a wide forest-tundra (see 5.2.4.6).

If vegetation, climate, and snow cover are as closely-linked as it appears (Hare and Ritchie 1972), then steep or gradual gradients of tree and upland tundra cover should correspond to steep or

gradual climatic and snow-cover gradients. Mean annual measured snowfall gradients (Figure 18 in Hare and Hay 1974) are steep in both the northwest and southeast and gradual between the geographic extremes (with the exception of the area east of the Coppermine River). Snow cover is deepest and lies longest over Keewatin and northern Manitoba.

Mean July air temperature on the ground and at the 850 mb level, mean date of rise of daily mean air temperature to 0 °C, and mean length of frost-free period (Figures 4B, 5C, 11, and 12 in Hare and Hay 1974) all show steeper gradients in the northwest than in the southeast. The zone of mixing of modified Pacific and Arctic air masses is narrow in the northwest and broad in the southeast (Figure 19 in Bryson 1966). April net radiation (Figure 28 in Hare and Hay 1974) in the southeast decreases sharply (from south to north) in the southern part of the forest-tundra. This likely correlates with the steep transition from dark canopy forest to snow-covered tundra seen in the southern third of the forest-tundra there.

Mean July air temperature on the ground and mean length of frost-free period decrease most rapidly in the northwest at the northern limit of the forest-tundra. This is presumably due both to the proximity of cold ocean waters off the arctic coast and to climatic feedback with the correspondingly steep vegetation gradient in the northern forest-tundra there.

A zone of colder air and deeper, longer-lying snow centered on the highlands near the headwaters of the Back River, Contwoyto Lake, and vicinity, coupled with the bedrock transition from

sedimentary to acidic crystalline rocks from west to east, may help explain the southward plunge of treeline east of the Coppermine River. Such climatic and snow cover gradients correspond with the observed upland tundra and tree cover gradients.

But it is noteworthy that the correspondence of gradients breaks down when two critical radiation parameters are compared to the vegetation cover. Mean annual absorbed global solar radiation and mean annual net radiation do not correspond well with the forest-tundra vegetation as they show steeper gradients over the southeast than over the northwest (Figures 25 and 29 in Hare and Hay 1974). Thus, the apparent paradox arises that the forest-tundra of the northwest, which generally spans 60-140 km, occupies a zone where net radiation gradients are gradual. In contrast, the forest-tundra of Keewatin and northern Manitoba spans 235-345 km yet occupies a zone of steep radiation gradients.

The apparent paradox can be partially resolved when narrower tree:upland tundra ratios are used for comparison with radiation gradients. In the southeast, the transition from a ratio of 10:1 tree:upland tundra cover in the south to 1:10 in the north takes place in 40-100 km. Relative to the overall width of the forest-tundra in the southeast, this vegetation gradient is steep and moreover takes place in the southern third of the forest-tundra where the mean annual net radiation gradient is also steep.

Allowing for the vagaries of interpolation and comparison, gradients of tree and upland tundra vegetation within the forest-tundra correlate reasonably well with synoptic climate.

Notwithstanding the clear correlations, synoptic climate cannot be expected to account for the variability in the dominant vegetation cover within the forest-tundra; this clearly derives from local and regional differences in the physical environment. More importantly, synoptic climate cannot fully account for the great width of the forest-tundra in the southeast and the steep transition in many places elsewhere. Topoclimatic and edaphic factors may help account for both the width of the forest-tundra and the location of steep vegetation gradients within it (see 5.2.4).

5.2.3 Cover structure of dominant forest-tundra vegetation

Gradual change at both high and low cover values and steep gradients between about 5-85% cover are approximated by a sigmoid curve. The sigmoid cover pattern appears to be a fundamental characteristic of spatial vegetation change in the forest-tundra. In the steep phase of the vegetation cover gradient, positive feedbacks between vegetation, climate, and snow cover may drive the landscape to a new equilibrium. The prime controls of tree and tundra cover at the extremes of the forest-tundra appear to be topoclimatic and edaphic factors.

Inspection of Figures 13, 14, and 20-25 indicates a definite pattern or structure to spatial vegetation change within the forest-tundra. This cover structure is best viewed in smoothed

transect diagrams (Figures 14A and 25A) which generally approximate 3-dimensional sigmoid curves.

Because the slope and form of the curves vary, it would be unreasonable to imply any mathematical precision to equations describing these gradients. The widespread occurrence of this sigmoid structure, however, suggests an underlying organization to spatial vegetation change within the forest-tundra. By analogy, the logistic growth equation of population ecology may be applied. Although rigor is not implied, change in percent vegetation cover over distance may be described as:

$$dN/dL = rN (1 - N/K)$$

where dN = change in percent cover of trees or upland tundra

dL = distance, in km

r = innate capacity of vegetation to increase in cover

N = present cover value

K = maximum cover possible on the landscape, set to 95%
since some small amount of wetland, shrubland, and
eroding terrain is always present.

The term N/K might be thought of as the bioclimatic resistance to change, or equivalently, the negative feedback within the system. As percent cover N nears its maximum value K , increase in cover slows, perhaps because the major bioclimatic feedbacks between vegetation, climate, and snow cover have already taken place. Macroclimatic constraints (e.g., maximum and minimum values

of radiant energy available to the region) are another form of control in the vegetation--climate system.

Table 6 presents data for rates of change of smoothed tree cover as depicted in Figure 25. As tree cover rises from north to south, change is at first slow as percent cover of trees is limited by frequency of favorable sites in a dominantly tundra landscape. In mid-range, tree cover rises rapidly to landscape dominance after which vegetation change slows. Thus from 5-10%, tree cover changes 0.44%/km (median); from 10-25%, change increases to 0.81%/km; steepest change occurs from 25-50% at 1.24%/km; from 50-80% change slows to 0.84%/km.

Heavy averaging of airphoto data did not permit depiction of smoothed cover contours above 80 or below 5%, but inspection of the 3-dimensional plot (Figure 25A) indicates slow changes in tree cover at both high and low cover. This is best seen in the northern half of the forest-tundra east of the central meridian and in the southern half of the forest-tundra west of the meridian.

When minimum averaging is used as in Figure 23B to depict tree cover, the 0 and 2% contours can be depicted. Note the gradual change at low cover values. Overall, the 0-2% transition spans a median 6.9 km at 0.29%/km, but there is wide variability (ST DEV/mean = 0.78), with gradual change in the southeast and sharper transitions in the northwest. For the sector SE from Point Lake to northern Manitoba, the 0-2% transition spans 11.5 km at a median 0.17%/km (n=37). For the sector from the Cordillera to Point Lake, the 0-2% transition is a much narrower 4.6 km at a median 0.43%/km (n=35).

Table 6. Rates of change of smoothed percent tree cover in the forest-tundra (average of 12 neighbors, as depicted in Figure 25).[#]

Interval (%)	dN (%)	dL (km) mean median	dN/dL* mean median	S.D. mean	S.D./ $\sqrt{n}$	r mean median	N/K [^]	n
5-10	5	9.8 11.5	0.51 0.44	0.39	0.05	0.06 0.05	0.11	67
10-25	15	17.0 18.6	0.88 0.81	0.38	0.05	0.05 0.04	0.26	64
25-50	25	18.2 20.1	1.38 1.24	0.62	0.09	0.06 0.05	0.52	53
50-80	30	36.7 35.8	0.82 0.84	0.33	0.05	0.06 0.07	0.84	42

[#] data for the 0-2% interval, derived from minimum averaged plot (Figure 23B):
 dN% = 2; dL mean, median = 5.0km, 6.9km; dN/dL = 0.40%/km, 0.29%/km; S.D. = 0.31;
 S.D./ $\sqrt{n}$ = 0.04; r mean, median = 0.20, 0.15; N/K = 0.02; n = 72

* F ratio for dN/dL (including the 0-2% interval) = 50.49, df factor = 4,
 df error = 293, $p < 0.0001$

[^] using N at upper end of interval, and K = 95 %

Upland tundra spatial vegetation change in the forest-tundra is similar, as Figures 13 and 14 attest. The pattern of gradual transition at both high and low cover values and steep gradients between about 5-85% repeats itself consistently. The sigmoid cover pattern appears to be a fundamental characteristic of spatial vegetation change in the forest-tundra.

In a logarithmic plot (Figure 24) the gradient is roughly curvilinear. The mathematical core of the gradient, within which the tree:upland tundra cover ratio changes from 10:1 to 1:10, ranges in width from 25-55% of the forest-tundra. In extreme cases, this gradient may span as little as 10% (e.g., northern Manitoba--southern Keewatin) or as much as 90% (e.g., Wopmay River, Artillery Lake) of the total width of the forest-tundra. The tails of the gradient, where the tree:upland tundra ratio is $>100:1$ and $<1:100$, occupy about 10% of the forest-tundra.

5.2.4 Climate and vegetation in regional perspective

A cardinal anomaly exists in the radiation budget of the forest-tundra of the NWT: the northwest functions on roughly 3/4 the mean annual net radiation available to central and southeast districts. Seven regional vegetation--synoptic climate anomalies are discernible.

As described above, the generalized orientation and steepness of vegetation gradients within the forest-tundra correspond

reasonably well with relevant climatic isopleths. Of equal interest are the areas where the vegetation apparently does not correlate well with synoptic climate.

At the extremes of the study region, in the great wetlands of the Mackenzie valley and the Hudson Bay Lowlands, the overriding controls of vegetation are edaphic. Super-abundant soil moisture, flooding, impeded drainage, shallow permafrost, and organic soils in these regions affect and are affected by vegetation in complex ways.

The distinctive lowland vegetation and terrain of both these regions sets them apart from the forest-tundra proper. In the Mackenzie Delta, Mackay (1974) identified spruce--willow--alder--poplar, willow--alder--poplar, and sedges--willow vegetation zones. For the Manitoba portion of the Hudson Bay Lowlands, Ritchie (1960a) delineated transitional, moss muskeg, treeless bog, and lowland complex vegetation zones. In neither region does a forest-tundra landscape exist. For vegetation and terrain relationships in these lowlands, see Kerfoot (1973), Lambert (1973), Zoltai and Pettapiece (1973); Mackay (1974), and Ritchie (1984) for the Mackenzie valley; and Ritchie (1957, 1960a, 1962), Brown (1973b), Zoltai (1973), Thie (1976), Dredge and Nixon (1979), and Mollard (1982) for the northern Hudson Bay Lowlands.

Outside the wetland and organic terrain of the Mackenzie Delta and Hudson Bay Lowlands, areas of apparently poor vegetation--climate correlation are numerous. It must be made clear, however, that due to topographic influences, local or regional vegetation and climate may actually correlate well. Although sparsity of

climatic data precludes direct comparisons, topoclimatic effects are the only logical explanation for many regional vegetation patterns.

Highlands account for most southern outliers of forest-tundra in the northwest, e.g., the Colville Hills (peaks >600 m, lying >300 m above the plain), the Norman Range (peaks >900 m, 750 m above the lowlands), highlands between Smith and Keith Arms of Great Bear Lake (e.g., the Scented Grass Hills which peak at 655 m, 500 m above the lake), and Grizzly Bear Mountain (plateau at 610 m, peak at 700 m). High elevations probably also account for southern extensions of low arctic in the Caribou Hills, south of the Dismal Lakes, and irregular contours elsewhere.

Topoclimatic influence is also implicated in the narrow width of the forest-tundra north of Dease Arm, Great Bear Lake, and from the Snare River SE to Great Slave Lake. In these regions, elevation rises north- or northeastward, creating steep topoclimatic gradients. Conversely, northward decrease in elevation may in part explain the northward extension of trees in the Thelon River area and the great breadth of the forest-tundra in SE Mackenzie District and Keewatin. In eastern Canada, Hare (1950) indicated that northward fall of elevation in Labrador-Ungava has the effect of partially offsetting the normal northward fall of temperature. As a result the thermally correlated zonal divisions of the boreal forest are wide there.

A cardinal anomaly exists in the radiation budget of the forest-tundra of the NWT: the northwest functions on roughly 3/4

the mean annual net radiation available to central and southeast districts. When a representative mean annual net isorad (20 kJ yr^{-1} after Hare and Hay 1974) is overlaid with the forest-tundra (Figure 24B.1), crossover of vegetation and radiation contours occurs in the central district north of Great Slave Lake. Other relevant isotherms and isorads show a similar diagonal orientation with vegetation contours. This vegetation--climate crossover coincides with a major landscape transition from sedimentary rocks overlain by fine-textured soils in the northwest to crystalline rocks overlain by coarse-textured soils on the Shield.

Seven regional anomalies not obviously correlated with synoptic climate are discernible even in smoothed depictions of upland tundra and tree cover (Figures 14, 25; see sections 5.2.4.3-9).

Explanation of these cardinal and regional anomalies implicates (1) topoclimate, (2) edaphic compensation or restriction, and (3) bioclimatic feedback. Evidence for edaphic controls is largely anecdotal. Numerous boreal species such as dwarf birch, black spruce, and *Vaccinium vitis-idaea* are restricted to cold acidic soils, bogs, mountaintops, or other islands of suitable habitat at the southern edge of their ranges, presumably due mainly to their inability to compete with hemiboreal species in other habitats. At their northern limits, many boreal plants such as black and white spruce, larch, *Salix planifolia*, and *Viburnum edule* are restricted to river valleys, stream and lakeshores, moist slopes, calcareous soils, etc. where presumably the boreal vegetation is responding more to abiotic factors than to competition. So consistent is this shift in biotope (physical

site) along climatic gradients that Walter (1979) has formulated a "law" which states that a change in biotope compensates as far as possible for a change in climate such that habitat or environmental conditions remain relatively constant.

In the case of forest-tundra vegetation, lack of physiological data precludes any fundamental explanations of biotope compensation or restriction. Vegetation-landscape patterns are highlighted below, while more basic explanations await detailed site and eco-physiological studies.

Before turning to anomalies it must be mentioned that meso- and micro-climatic influences militate against the use of synoptic climatic data in interpreting local conditions. Climatic differences between adjacent open and closed crown forest, or between north- and south-facing slopes, can be equivalent to tens or hundreds of km of macroclimatic gradient (Hare, pers. comm.). Moreover, in areas of low hills, standard adiabatic cooling does not apply. Mean temperatures of depressional areas may be several degrees lower; and use of adiabats, which apply for large elevation differences, might result in serious errors (Huovila 1970). Summer temperatures of slope bases and valleys are on average colder than those of hilltops and flat terrain (Dolgin 1970; Huovila 1970).

5.2.4.1 Radiation budget

Compared to that of the southeast, both lower temperatures and absorbed solar and net radiation values are characteristic of the forest-tundra of the northwest. The northwest receives an average 15 kly mean annual net radiation as compared to 20 kly in the southeast. The southern portion of the forest-tundra across much of the central district is anomalously warm.

Mean annual heating deg-days (0 C base; see Table 5) for the forest-tundra indicate that the northwest is colder than central and southeast districts. The northern limit of the contiguous forest-tundra corresponds to heating deg-days values of 3400-4100 in the northwest; ranges from 2800-3500 deg-days between Great Bear Lake and Keewatin; and from 3000-3600 in the southeast. The southern limit corresponds to about the 2800-3400 deg-days isotherms in the northwest; ranges from 2300-2800 deg-days in the central district, and 2600 deg-days in the southeast. By rough approximation, the northern limit of much of the forest-tundra SE from Great Slave Lake to Hudson Bay is as warm as the southern limit of the forest-tundra in the northwest. The southern portion of the forest-tundra across much of the central district (NE of Yellowknife and SE of Great Slave Lake) is anomalously warm.

April net radiation for the northwest approximates 15-35 ly/day, and those for east of Great Bear Lake to Hudson Bay lie between 30-75 ly/day.

Isorads of annual mean absorbed solar radiation for the subarctic NWT are offset at a slight diagonal to the vegetation zones, with lower values of about 52-55 kly for the northwest, and higher values of about 53-63 kly between Great Bear Lake and Hudson Bay.

The forest-tundra of the northwest is characterized by a mean annual net radiation of 12-18 kly, and an average of 15 kly (potential evaporation -25 cm). The forest-tundra dips sharply southward east of the Coppermine. From the Coppermine River to the Keewatin border, the forest-tundra receives a net annual radiation of 17-23 kly, with a mean of about 21 kly (PE -36 cm). Southern Keewatin and northern Manitoba receive 15-25 kly of net radiation, with an average near 20 kly (PE -34 cm). It appears that the forest-tundra of the northwest functions on roughly three-fourths the mean annual net radiation available to central and southeast districts.

It is noteworthy that a lower cardinal temperature of 15 C has been shown important in determining the timing and success of seed germination in black spruce (Black 1977), and this may explain the absence of black spruce across much of the forest-tundra of the northwest (see Table 5). However, edaphic controls are indicated in that the northern limits of both black and white spruce on the Shield lie climatically south of their respective northwestern limits.

5.2.4.2 Edaphic controls

Edaphic restriction or compensation may not only help to explain the cardinal climatic anomaly of the forest-tundra, but also the relative locations of steep vegetation gradients within the transition zone and its general increase in width from northwest to southeast. Further evidence in support of edaphic influences is provided by a comparison of vegetation and landscape within the Soviet forest-tundra.

The preceding climatic data, however approximate, illustrate the climatic anomaly that exists within the forest-tundra. This anomaly might be explainable, in part, in the context of edaphic controls. The "law of the minimum", first described by von Liebig in 1840, might be stated as: "the growth and/or distribution of a species is dependent on the one environmental factor most critically in demand." (Barbour et al. 1980:28; see also Fritts 1971:424-427). There are important modifications to the law of the minimum in that environmental factors act mutually as a concerted force (Cain 1944): a low level of one factor can sometimes be compensated for by optimum levels of other factors, and, the effects of one factor can be magnified as other factors reach maximum or minimum values (Barbour et al. 1980). Edaphic control is second only to climate in shaping the areal pattern of vegetation (Cain 1944).

Crossover of relevant thermal and radiation isopleths with vegetation cover contours coincides with a major landscape

transition. To the NW of the Coppermine valley, the forest-tundra is underlain by predominantly sedimentary rocks overlain by silt loams and clay loams. To the SE, the bulk of the bedrock is acidic crystalline and typical soils are sandy loams and loamy sands. It is possible that northwestern soils might act in compensatory ways to allow the existence of forest-tundra well to the north or, conversely, poor soils might limit forest growth south of its climatic potential in central and southeast districts. Data supporting such an interpretation are largely circumstantial but merit attention.

In one quantitative study of forest-tundra vegetation near McTavish Arm, Lindsey (1952) demonstrated relationships between bedrock lithology and tree density. On relatively level (slope <2%) domes and ridgetops with much bare bedrock, the lowest density of white spruce was found on granite (3 trees/ha), followed by 9 trees/ha on related acidic rhyolite porphyry; on arkose conglomerate tree density reached 24/ha, while maximum density was found over intermediate to basic trachyte and andesite at 36 trees/ha.

As shown in section 4.4, the typical loamy till soil of the northwest is slightly higher in pH and has much higher CEC and nitrogen and potassium levels than the sandy loams and loamy sands of the Shield. Fine-textured loams also retain more freely available water than sandy soils, and moist soils retain trees farther to the north than dry soils (see section 5.3). Because they retain more water which evolves latent heat of fusion, freezing and thawing occur later in fine-textured soils than in

coarse soils (Geiger 1965; Viereck 1970). Indeed dry coarse-textured soils are among the first to lose their trees at the southern edge of the forest-tundra, as has been described for ancient beach ridges on McTavish Arm (Lindsey 1952). It is also relevant that forest-tundra soils in the northwest typically have thinner active layers than sandy Shield soils, thus creating perched water tables with abundant liquid water in summer.

It may be that this combination of greater nutrient status and more available water in loamy soils compensates for the lower temperatures and net radiation of the northwest. Although the physiological basis of edaphic compensation is virtually unstudied, further evidence is provided when the northern portion of the forest-tundra extending east from Dease Arm through the Dismal Lakes to the Coppermine River is considered.

While this region is nominally Shield, bedrock is primarily sedimentary, soils are predominantly fine-textured loams, and available data indicate a pH of 7-8. Thus these soils are nearly identical to fertile soils in the northwest, and here the forest-tundra extends climatically far north before plunging southward at a transition to crystalline Shield rocks and rising elevation. Two other major areas of high tree cover that are nominally Shield but also underlain by sedimentary and/or volcanic rocks are the Thelon River and the Henik Lakes.

It is relevant that the forest-tundra of the study region is underlain by widespread to continuous permafrost (Brown 1970, 1973); "treeline" (of Brown 1970) lies about 300 km north of the discontinuous/widespread permafrost transition. Much of the

forest-tundra of the northwest lies in the continuous permafrost zone. In marked contrast, treeline on the Shield rockland of Labrador-Ungava lies about 300 km south of the discontinuous/widespread permafrost transition (Brown 1970), and extends northward on the sediments of the Labrador Trough.

Further indirect evidence supporting edaphic control is given by geographic variation in width of the forest-tundra and the relative locations of steep vegetation gradients. Thus edaphic restriction or compensation may not only help to explain the cardinal climatic anomaly of the forest-tundra, but also the relative locations of steep vegetation gradients and the general increase in width of the zone from northwest to southeast.

Theoretically, on poor sandy soils in the forest-tundra, edaphic conditions should exert a stronger control over tree distribution than on rich well-watered soils. Trees on terrain of low soil quality would be found primarily in the patchwork of sites where moisture, nutrients, snow cover, etc. are amenable to reproduction and survival. These sites might support trees up to their climatic limits, but most of the landscape would become treeless sooner and thus the forest-tundra would be located farther south than on terrain of high soil quality. The position of the forest-tundra, and vegetation gradients within it, corroborate these theoretical vegetation patterns.

On the relatively rich loamy soils of the northwest, the forest-tundra transition is narrow and located well north as many sites retain trees till climatic thresholds are reached (Figure 24). Conversely, on the generally poor but heterogeneous terrain

of the Shield, steep gradients in tree and upland tundra cover take place in the southern forest-tundra, with a patchwork of sites retaining trees well to the north (Plate 8). This corroborates a "theoretical tree line" for southern Keewatin calculated by extrapolation of black spruce growth indices (Mitchell 1973:Figures 2-4). This theoretical treeline lies about 290 km NE of the "actual tree line" (~ the zone of steep vegetation gradients), and close to the absolute limit of trees as determined in this study. Here the forest-tundra is broad and lies, for the most part, climatically south of its potential. This is by far the predominant forest-tundra vegetation pattern on the Shield, especially in the southeast.

Further evidence in support of edaphic influences is provided by comparison of subarctic soils, vegetation, and climate in the Soviet Union (Lavrenko and Sochava 1954; Nalivkin 1960; Sachs and Strelkov 1960; Academy Sciences USSR 1963; Lydolph 1977). The forest-tundra of the USSR is broadest ($\sim 100 \pm 60$ km S.D., as delimited by Lavrenko and Sochava) where it lies "south" of its climatic potential. These regions lie (a) east of Cheshskaya Guba and west of the Urals (65 ± 20 km wide), and (b) east of Obskaya Guba to about 120 km east of the Yenisey River (140 ± 60 km wide). Both of these regions were glaciated during Late Pleistocene Sartan (= Late Wisconsin) time (Velichko 1984); both are broad, generally low-lying plains having a high areal cover of *Sphagnum* bogs. Mineral soils are developed primarily on late- and post-glacial sandy loam and sandy fluvial and lacustrine

deposits; permafrost is scattered to widely distributed (Lydolph 1977).

In contrast, most of the forest-tundra between the Yenisey and Kolyma Rivers has been unglaciated for at least 23-50,000 yrs (cf. Lavrenko and Sochava 1954; Velichko 1984). The generally narrow subarctic forest-tundra there (50 ± 30 km wide) is underlain by primarily Cretaceous, Triassic, and Jurassic sediments, with Quaternary alluvium and lacustrine sediments prominent only between the Yana and Kolyma Rivers (Nalivkin 1960). The climate of the Yana-Kolyma forest-tundra province is harsh; its topography is one of poorly-drained plains with many lakes; permafrost is continuous and >250 m thick; soils are predominantly gleysolic cryosols, indicative of fine soil textures (see Academy Sciences USSR 1963; Karavaeva and Targul'yan 1969; Lydolph 1977); the forest-tundra spans only 40 ± 20 km. It is likely that soils in eastern Siberia, where the forest-tundra is narrow and reaches far to the north, are generally finer in texture than those in regions where forest-tundra lies south of climatic potential.

5.2.4.3 McTavish Arm, Great Bear Lake to east of the Coppermine River

High tree cover in this area may be correlated both with lower elevations and soils underlain by sedimentary rocks.

High tree cover extends eastward from McTavish Arm to a limit

west of Takiyuak Lake and eastern Point Lake (Figure 25). Both topoclimate and parent materials/soils appear to be involved in this noteworthy vegetation pattern.

Elevation rises eastward from 156 m at Great Bear Lake to 300 m in about 10-25 km, and continues to rise to 460 m in another 40-60 km. Elevations plateau between 425-500 m for 40-50 km then fall to about 400 m in the broad valley of the upper Coppermine. East of the Coppermine, trees do not rise above 450 m elevation.

Coincident with this elevation gradient is an eastward transition from acidic Archean crystalline rocks east of McTavish Arm to Archean sediments and metasediments overlain by basic silt loams in the Coppermine River region. The limit of trees east of the Coppermine generally parallels a transition back to acidic crystalline rocks.

It is likely that the low elevations and rich silt loams of the upper Coppermine River region permit a high cover of trees. East of the Coppermine the rise in elevation and return to a band of acidic crystalline rocks likely combine to eliminate trees from the landscape.

5.2.4.4 Snare to Rocknest--Point Lakes

Tree and upland tundra patterns in the Snare to Rocknest--Point Lakes region correlate with elevation and parent material changes. A decrease in tree cover north from Snare Lake is followed by a sharp rise in trees that occurs south of Rocknest

and Point Lakes. Details relating elevation, bedrock, soils, vegetation, and cover gradients have been described in section 4.3.16 (Figure 23C, Plate 2). Suffice here to note that smoothed tree cover (Figure 25) reaches zero on the plateau between Snare and Rocknest--Point Lakes. Tree cover then rises northward with a combined fall in elevation and transition from sandy brunisols over Archean gneisses to rich silt loams overlying mainly sediments and metasediments.

5.2.4.5 Thelon River

The possibility that trees on the Thelon and its tributaries are relictual appears unlikely. Northward fall of elevation, relatively protected valleys with well-watered slopes, glaciolacustrine submergence, alluvial soils, and bioclimatic feedback may all contribute in inter-related ways to account for this most remarkable peninsula of the forest-tundra.

Of all northern extensions and outliers of the forest-tundra in the NWT, the Thelon is perhaps the most striking. In spite of this, the vegetation of the Thelon remains unstudied in any systematic way. The fact that peak tree cover (10-20%) along the Thelon valley occupies an "island" from north of 64°N to upstream of the Ursus Islands suggests these tree stands are relictual outliers, but evidence for this is lacking.

Clarke (1940), whose study of the Thelon Game Sanctuary remains

the best reference for the area, concluded that tree stands on the Thelon are more often expanding than contracting in area. He surmised that Thelon forest stands must have looked much as they did in 1940 for hundreds of years. Other workers have noted the vigorous growth and reproduction of trees along the Thelon (E. Kuyt, pers. comm.; C. Norment, pers. comm., in Larsen 1980; Zoltai, pers. comm;).

Air and ground level photos indicate well-developed forest on the river flats of the Thelon and its tributaries (this study). Although ground level information is scant, study of airphotos shows white spruce to be the predominant tree in forest stands along the Thelon. Tall trees with spire-like crowns indicate vigorous growth rates in many stands. Black spruce and larch occur along with white spruce, and large numbers of seedlings have been reported in many stands (Clarke 1940; C. Norment, pers. comm., in Larsen 1980). E. Kuyt (pers. comm.) observed some black spruce on slopes and balsam poplar on alluvium; at Lookout Point, some white spruce measured 40 cm diameter at the butt. S. Zoltai and E. Kuyt (both pers. comm.) indicated that spruce cloning probably takes place (on cryoturbic wet soils), but the commonness of such spruce clones was not assessed (see Plate 11).

On the whole, tree stands along the Thelon and its tributaries, at least in the absence of disturbance, presently seem capable of maintenance and even expansion in area. Careful study will be required before any conclusions can be made regarding stability and the former extent of forest on the Thelon.

A consideration of the Thelon landscape may shed some light on

the problem. Parent materials are of two major kinds: red till derived predominantly from Dubawnt sandstone; and alluvium. The red till reported on (Bradley et al. 1982) does not differ appreciably from a typical Shield till, being sandy loam to sand in texture, having a pH of 4.7-5.9 in the C horizon, and a CEC of 0.2-2.8 meq/100 g for various horizons. Percent nitrogen is perhaps slightly higher than in Shield tills (trace to 0.2%).

Both sandy and silty alluvium are found along the Thelon and its tributaries (Clarke 1940; airphoto observ.), but no data exist on its chemistry. The entire Thelon valley was subject to glaciolacustrine submergence (Geological Survey Canada 1967). Although pre-existing landforms were not appreciably changed (e.g., beaches parallel drumlin contours), the extent to which submergence may have altered surface horizons in the parent materials is not known.

Clarke (1940) observed the most luxuriant growth of spruce along the Thelon in a place where springs emerged from sandstone, and on the silty alluvium of Finnie River flats where white and black spruce and larch form an extensive stand. The heaviest forests occur on alluvium, grading upward into forest-tundra on the gentle valley slopes of the Thelon and elsewhere (airphoto observ.). Well-developed white spruce forest is found on alluvium in the valley of the Clarke River near 104°W.

Topography and elevation may also play roles. The valley of the Thelon and its major tributaries such as the Clarke, Finnie, Tamarvi, and Kigarvi Rivers are protected relative to the treeless interfluves. Average mean elevation for the Thelon

valley north of 64°N is 150 m, 60 m lower than mean elevation out of the valley. Average minimum elevation is 120 m, also 60 m below minima out of the valley. Such elevation differences translate to a temperature difference of 0.5 C (based on a summer lapse rate of 0.8 C/100 m; see Burns 1974). Mean elevations outside the valley lie 90 m above average minima in the valley, corresponding to a temperature difference of 0.7 C. Whether elevation differences of 60-90 m would be offset by cold air drainage would depend on the form of the valley and exposure to wind.

Northward fall of elevation may compensate at least partly for latitude. Mean landscape elevation near Howard and Lynx Lakes on the upper Thelon is 370 m. By comparison, mean elevation of the Thelon north of 64°N is 220 m lower, and its average minimum elevation 250 m lower. By lapse rate alone the northward fall in elevation translates to a temperature difference of +1.8-2.0 C. When compared to mean July temperatures for eastern Mackenzie District (Figure 5 in Hare and Hay 1974) a 2 C difference corresponds to 300 km of SW--NE gradient (1 C/150 km). By further comparison, the upper forest limit in the mountains of the USSR rises N--S about 100 m/deg latitude (Gorchakovsky and Shiyatov 1978), which converted to summer lapse rate approximates 1 C/140 km. Although highly approximate, the calculation indicates that northward fall of elevation may make the Thelon valley something of a thermal oasis.

Bioclimatic feedback between vegetation, snow cover, and radiation may also be important. In the main "island" of trees

and tall shrubs along the middle Thelon mean tree cover is 14% and shrubland cover is 6%. Thus 20% of the landscape has a relatively low albedo and a rough surface capable of lodging snow and decreasing wind. Also, runnel occurrence is higher along the middle Thelon than on typical Shield terrain (Figure 5), indicating long well-watered slopes and perhaps finer soil texture than those of red till.

5.2.4.6 Great Slave Lake to eastern Keewatin--Manitoba

Edaphic controls, and topoclimatic effects are offered as an interpretation for the great breadth of the southeastern forest-tundra.

The forest-tundra increases dramatically in width from the East Arm of Great Slave Lake (70 km minimum) to eastern Keewatin--Manitoba (345 km maximum). It is unlikely that synoptic climate can wholly account for this pattern (see 5.2.4.1-2). While the northern forest-tundra (lying north of the core of steep cover gradients) has been considered relictual, there are difficulties with this view (see 5.1). An alternate interpretation of the forest-tundra cover pattern involves edaphic controls and the NE fall of elevation.

On the typically nutrient poor, drier, sandy soils of the Shield, edaphic restrictions may elicit steep gradients in vegetation cover in the southern forest-tundra. Low tree cover

extends northward, perhaps in the mosaic of higher quality sites, till climatic thresholds are approached, resulting in a wide transition zone (see 5.2.4.2 for a discussion of edaphic controls).

The NE fall of elevation may also contribute to the wide forest-tundra. On average, elevations fall 100-150 m from SW to NE, corresponding to a compensatory summer warming of ~ 0.8 - 1.2 C (using the 0.8 C/100 m summer lapse rate of Burns 1974). July mean temperature for the wide southeastern forest-tundra ranges from 11 - 13 C (Table 5); thus, a 1 C compensatory summer warming might contribute to the gradual vegetation gradients.

An exception to the NE fall of elevation provides further indication of topoclimatic effects: the highland between Nueltin Lake and the Watterson--Hicks Lakes area is characterized by a steep fall in tree cover (Figure 25B; see also 5.2.4.8)

5.2.4.7 Kamilukuak Lake to Kazan River

High tree and shrubland cover may be due in part to the abundance of well-watered sites and to the NE fall of elevation. Bioclimatic feedback may contribute to render the local climate more suitable for forest and shrubland than would appear from the synoptic level.

The area lying between 102 - 100° W, south of Kamilukuak, Nowleye, and Angikuni Lakes, and north of $61^{\circ} 30'$ N supports an

unexpectedly high cover of trees and shrubland. Trees there include black and white spruce and larch. Mean and median tree cover for the area are 8 and 6%, and those for shrubland are 7 and 5%. Peak tree cover is reached both east and west of the Kazan River near latitude 62°N. at 14-23%, while that for shrubland in that area ranges from 5-23%.

Bedrock is predominantly Archean granitic gneisses, with lesser amounts of Proterozoic acidic volcanics, Archean granite, paragneiss, and paraschist (Geological Survey Canada 1968) which shows little or no correlation with the vegetation patterns. The land slopes to the NE, falling about 60-100 m in about 80 km. Such an elevation fall may contribute to the high tree cover.

It is noteworthy that shrubland attains such high cover, indicative of well-watered sites, and that tree cover should be closely correlated with shrubland cover. For the 15 sample airphotos in the area, tree and shrubland cover were positively correlated at $r=0.70$, $0.01 > p > 0.001$. Topographic locations listed for spruce and larch on the airphoto notes for the area are, in decreasing order of preference: drainages, slopes and slope bases, shores, low-lying areas and depressions (including some dominated by larch), low summits, and pitted outwash.

High tree and shrubland cover may be due in part to the abundance of well-watered sites. Combined tree and shrubland cover in the core area ranges from 20-45%; thus bioclimatic feedback may contribute to render the local climate more suitable for forest and shrubland than would appear from the synoptic level.

5.2.4.8 Nueltin--Hicks--Henik Lakes region

High elevation, granitic bedrock, and thin surficial cover may help account for low tree cover in the Nueltin--Watterson--Hicks Lakes area. Farther east, low elevations, soils derived from sedimentary and basic volcanic rocks, and an abundance of well-watered slopes may help account for the zone of high tree cover in the Henik Lakes area.

No single landscape factor can be identified as more important than others in accounting for areas of high tundra or tree cover in the Nueltin--Hicks--Henik Lakes region (Figure 25B). In the Nueltin Lake area, bedrock changes are correlated with elevation gradients such that highlands are underlain by Archean granites while lower elevations are underlain by Archean crystalline gneisses, sediments, metasediments, and basic volcanics. In this area tree contours roughly parallel those of elevation and bedrock, with tree cover falling below 2% near the 300 m contour and transition to granite bedrock. In the Windy Bay area at the NW end of Nueltin Lake, F. Harper (pers. comm., in Porsild 1950) reported that black spruce is the dominant tree, associated with larch in "muskegs" and on upland slopes; white spruce is sparse and local, and paper birch and balsam poplar are rare; most trees do not exceed 7.5-9 m ht; "barren grounds" cover 80-90% of the land.

Thin surficial cover over bedrock likely helps account for the low tree cover in the Watterson--Hicks Lakes area.

In the region as a whole, low tree cover is associated with granites and crystalline gneisses and higher tree cover with sediments, metasediments, and basic volcanics (airphoto observ.). The correspondence between bedrock and vegetation gradients is not sharp, however, and it is likely that glacial dispersion has blurred the relationship between soils and underlying bedrock. Soils data are too few for comparison between areas (see Hardy 1976; Zoltai and Johnson 1978), but it is clear that regional bedrock and glacial flow patterns together can have a significant influence on the chemical properties of the till and associated surficial deposits of that region (Shilts 1980).

Elevations fall from +300 m east of Nueltin--Watterson Lakes to below 150 m east of the Henik Lakes, corresponding to a compensatory summer warming of ~ 1.2 C across 110-120 km. Runnels and slopewash are abundant in the area (Figure 5), indicating extensive well-watered slopes. Tree cover peaks below the 230 m contour at $\sim 20\%$ in the vicinity of South Henik Lake, Kognak River, and Tatinnai and Roseblade Lakes. Black spruce is more abundant than white spruce, and larch is locally dominant.

5.2.4.9 SE Keewatin and NE Manitoba

The landscape transition from uplands to poorly-drained lowlands and organic terrain depresses potential upland tundra cover by preemption, and probably contributes to low tree cover

also. The climatic effects of Hudson Bay are possibly the prime agents depressing tree cover as the bay is approached.

The limit of trees drops abruptly SSE along a line east of 96°W, lying between the 150-75 m contours in SE Keewatin, and reaching the shore of Hudson Bay a short distance north of the Caribou River, northern Manitoba. There black spruce and larch are the dominant trees; white spruce is best developed along water courses and the margins of glaciofluvial deposits, and evidently forms the last outposts of trees in the Kinga Lake area (Hardy 1976; airphoto observ.).

Tree and upland tundra contours show no clear relationship to the limit of post-glacial marine overlap (cf. Geological Survey Canada 1967). Isostatic rebound may be related in some way to the vegetation patterns, particularly around 60°N where the limit of trees lies close to Hudson Bay. Along the west shore of Hudson Bay approximate rebound has been 150 m (Nichols 1976) in 7500 yrs (Bryson et al. 1969), or about 2 m/century.

Below the 150 m contour and roughly correlating with the limit of trees, wetland increases sharply in cover from +10% in the west to >25 and even >50% in the east, where it comes to dominate the landscape. By the shores of Hudson Bay, unaveraged wetland cover rises to >75%. Countless ponds and small lakes dot the landscape along the wetland dominated margin of Hudson Bay. Much of this wetland is likely incapable of supporting trees regardless of the climate.

The distance to which cold moist marine air, derived from

Hudson Bay and Arctic Archipelago source regions (Bryson 1966), extends inland is an open question. The 10 C mean July air isotherm plunges south upon reaching Hudson Bay (Figure 5C in Hare and Hay 1974), as does the 60 day contour for frost-free period (Figure 12 Hare and Hay). Such a deterioration of the growing season may be important, but it is noteworthy that much of the forest-tundra of the northwest experiences an even shorter frost-free period.

In the USSR, the forest-tundra is oriented parallel to the shores of the Arctic Ocean, and extends northward to the world's most northern forests (72°40'N) on the broad Taimyr Peninsula; in contrast, cold arctic waters and persistent ice contribute to the southward plunge of the forest-tundra west of Hudson Bay (Tikhomirov 1970). Similarly, the forest-tundra in eastern Canada extends farthest north near the center of the Labrador-Ungava peninsula, and extends southward along the shores of Hudson Bay and the Labrador Sea (see Payette 1983: Figure 3).

5.3 Tree and tundra landscape patterns at the extremes of the forest-tundra

While growing conditions for adult trees are not conducive to rapid growth on wet and summer-cold soils, conditions for seed reproduction and cloning seem favorable. The treelessness of dry soils at the southern limit of the forest-tundra may result from

frost and desiccation injury to seedlings during germination and establishment. Initiation by fire of upland "tundras" on dry summits may contribute to the landscape pattern.

Most black spruce, white spruce, and larch stands at their northern limits in the NWT occupy wet to wet-mesic mineral soils (Plates 1,6,9,10). Even newly-established stands are most often found on moist soils, so the relationship does not appear to be a matter of autogenic site "deterioration" (cf. Kryuchkov 1970, 1978). Whether this pattern constitutes a compensatory ecological shift in site preference or a narrowing of niche width is not clear. Preferred sites are slope bases, shores, and along drainages; when associated with glaciofluvial deposits, trees are found on esker and outwash flanks, or at pond edges in pitted outwash.

The fact that trees at their northern limits are often found growing along lakeshores indicates that factors other than growing season deg-days may be involved. Would a delayed spring and cooler summer temperatures nullify the positive effects afforded by the lake's environs? The moist soils typical of lakeshores, enhanced protection against fire, frost protection during the growing season, and perhaps insulation against winter and spring climatic extremes afforded by an accumulation of windblown snow, may all contribute to survival and maintenance.

It is noteworthy that outlier stands can be found growing in unprotected places such as exposed slopes, but these stands rarely lack a drainage or runnel in the center of the stand, or evidence

of poorly-drained soil conditions (gleying, mottling, tall willow and birch shrub). Prest (1985) found the northernmost spruce in the Bebensee Lake area (at 67° 21'N, 118° 19'W) on a "seemingly unprotected knoll" alongside a large aufeis.

In contrast, tundras at their southern limits are typically restricted to upland summits and dry, coarse-textured soils such as sands, gravelly sands, and stony and bouldery tills. A similar edaphic pattern has been noted in the recent rise in the birch (*Betula pubescens*) treeline in the Swedish Scandes: the rise in treeline was halted wherever a plano-convex landform, with little snow accumulation and low soil moisture conditions, was reached (Kullman 1979).

Fire may also play a role in this landscape pattern. Payette (1983) has noted that tree stands in the northern forest-tundra of Québec are strictly located in lowlands; interfluves are covered by dwarf birch/heath/lichen tundra with sparse black spruce clones. Initiation of the upland tundras, both in the northern and southern forest-tundra there, is believed related to fires followed by absence or low level of tree regeneration on exposed uplands. Yet the question remains as to why forest stands in lowlands can continue to regenerate while seedlings fail to establish on nearby uplands. While some upland tundras and pseudo-tundras at their southern limits in the NWT and northern Manitoba owe their origin to fire, most uplands at the northern limit of the forest-tundra show no signs of ever having burned. Thus, while fire is likely contributory to the lowland--tree stand

landscape pattern in the study region, it cannot wholly account for it.

On acidic terrain, sandy treeless sites at the southern limit of the forest-tundra are often covered by *Vaccinium vitis-idaea* --*Empetrum/Cladonia*--*Stereocaulon*--*Polytrichum* communities with occasional bare ground (see section 4.6). On stony acidic tills, ericad/lichen tundras are common, passing into lichen tundras as stoniness increases. On basic terrain, *Dryas*/lichen communities predominate. Regardless of pH, grass cover may be prominent on dry coarse-textured soils (*Agrostis borealis*, *Calamagrostis purpurascens*, *Festuca brachyphylla*, *Hierochloe alpina*, and *Poa* spp.).

The restriction of tundras at their southern limits is the corollary of the tree-wet mineral soils pattern. Causative factors are likely the same in these patterns, with trees and tall shrubs favored at the wet-mesic extreme and low shrubs and lichens favored at the xeric extreme. Thus, accounting for one landscape pattern may help account for both. The discussion that follows focuses on the tree-wet mineral soils pattern.

This landscape pattern, when noted in the past, has been attributed to restriction to warm summer micro- and meso-environments, to avoidance of winter wind, and to fire effects. Summer warmth in these generally depressional areas, however, is apparently not of prime importance to the trees. Temperatures of locations only 30 m apart in elevation may be negligibly different on clear days, but Huovila (1970) found lower areas to be as much as 7 °C colder on clear calm nights. In summer, minimum

temperatures on hilltops may be 2 C higher, and those in valleys 1.5-4 C lower, than those of flat terrain (Dolgin 1970). Thus, summer temperatures of depressional and valley tree outliers may be lower than those of surrounding tundra uplands.

Winter desiccation has been implicated as the primary cause of injury at the northern forest limit (Tranquillini 1979). Damage has been attributed to failure of new shoots to mature sufficiently during the growing season (e.g., thickening of the cuticle), and thus to transpire excessively during winter (Tranquillini 1979, 1982). Wardle (1981) presented data that suggest tissue freezing rather than water stress may be the prime cause of desiccation in inadequately hardened "krummholz" shoots of *Picea engelmannii* and *Pinus contorta*. Marchand and Chabot (1978) also question the water stress view, and in the case of timberline on Mt. Washington, N.H., cite evidence that inhibition of megaspore mother cell division and poor recruitment may better account for timberline position.

The dehydrating effects of winter winds are difficult to evaluate, and may be species-specific. Winter wind exposure of *Picea engelmannii* and *Abies lasiocarpa* shoots is a prime cause of needle dehydration and death, even in the absence of predisposing sub-optimal growing conditions (Hadley and Smith 1986). In contrast, exposure to winter wind does not increase frost desiccation in hardened black spruce (Marchand and Chabot 1978). Wind evidently reduces transpiration losses when leaf diffusive resistances are high, and perhaps even when diffusive resistances are low, attributed by Marchand and Chabot to

convection of heat from the leaf which lowers leaf-air temperature and vapor pressure gradients. Black spruce branches damaged by snowblast are evidently more susceptible to water loss than undamaged branches (Marchand and Chabot 1978).

If desiccation were an important limiting factor at the subarctic limit of trees, it is surprising that extensive fieldwork should find little evidence of brown winterkill. Dieback of leaders and pruning of branches near winter snowpack level was observed occasionally in exposed places, related to snow abrasion.

While protection from winter desiccation may be of some advantage, especially to seedlings, what other advantages might wet soils offer? Summer soil water potentials may be non-limiting to dry matter production at treeline (Vowinckel et al. 1975; Tranquillini 1979), but summer drought has been implicated in early cessation of elongation growth in white spruce (Scott et al. 1987b). Wet soils may confer some small photosynthetic advantage to outlier trees, but this advantage might be nullified by their typically lower soil temperatures, which depress elongation growth (Scott et al. 1987b), and inhibit dry matter production by depressing photosynthetic rates (Tranquillini 1979).

Factors favoring vigorous growth may not favor good regeneration. Maini (1966), in a study of forest-tundra in SE Mackenzie District, found that white spruce grew most vigorously on dry-mesic soil and black spruce on mesic soil, but best regeneration and highest density of both species were found on wet-mesic soil. Mineral soil or moist moss have been identified

as good seed beds for black spruce; its first year seedlings seem unable to control water loss; water stress and heat girdling are prime causes of mortality (Black 1977). Experimental removal of a *Cladonia stellaris* lichen mat brought about a steady decline in branch growth of black spruce seedlings over four years; the decreased growth was tentatively attributed to decreased soil moisture and/or loss of nutrients (Cowles 1982). White spruce seedlings require an uninterrupted adequate supply of moisture (Sutton 1970). Hot dry soils are inhospitable to white spruce seedlings at treeline (Scott et al. 1987b).

Although viable seed would be produced in outlier stands only during unusually favorable summers, germination and establishment might be more successful on their moist soils than on nearby dry soils. Vegetative reproduction in both spruces is, moreover, common on moist soils and rare on dry soils. Thus, it seems likely that conditions for both sexual and asexual reproduction are most favorable on these wet or wet-mesic soils. While growing conditions on nearby better-drained warmer soils are likely superior for adult trees, those conditions are unavailable if spruce and larch seedlings are unable to establish. Without abundant soil moisture, germination would probably not occur (Kullman 1979). Once established, trees may persist after the climate has deteriorated and further establishment has ceased (Black 1977; Kullman 1979; Scott et al. 1987a). Adult trees apparently possess greater resistance to climatic stress than do juveniles. Limits to physiological tolerances are most often exceeded during seed production, germination, and establishment;

these most sensitive stages set the limits for maintenance and spread of a species (Larcher 1980:47; this is Thienemann's Rule (see Thienemann 1956); in relation to treeline, see Black 1977; Kullman 1983, 1986).

Another advantage wet mineral soils usually offer over freely-drained soils is more abundant available calcium and magnesium (Larsen 1980). Hustich (1953), Daubenmire (1959), Larsen (1974), and others have noted a preference for calcareous soils in white spruce, *Larix sibirica*, and other trees near their northern or altitudinal limits. Throughout its distribution, *Larix lyallii*, in contrast, seems to prosper only on acidic soils low in calcium carbonate (Arno and Habeck 1972). The physiological basis for preference or avoidance of calcium-rich soils by trees has not been elucidated.

Freezing resistance of well-hardened northern spruce, larch, jack pine, paper birch, aspen, and balsam poplar are sufficient to ensure survival down to -70 or -80 C; or in some cases even immersion in liquid nitrogen (-196 C) after appropriate hardening (Sakai and Weiser 1973). Protection from winter cold is thus not a factor after hardening is complete. However, some of these species may become frost-sensitive in summer and suffer damage when temperatures dip below freezing (Tranquillini 1979). High air temperatures in May are detrimental to *Picea abies* as they promote premature initiation of growth with consequent increased risk of frost damage (Kullman 1986). The preference of treeline *Picea abies* for dense *Betula nana* thickets may be due to

reduced danger of frost damage to saplings during the growing season (Kullman 1986).

Hardening proceeds in a stepwise fashion promoted by decreasing temperatures (Larcher 1980). Site conditions in these outlier stands may permit more complete maturation and hardening than possible on dry soils. Incomplete hardening or immaturity of new growth may endanger susceptible parts, but frost damage *per se* does not appear to threaten survival of adult trees, at least at the alpine timberline (Tranquillini 1979).

Soils in outlier stands differ in two ways from the surrounding upland tundra soils: they are wetter and tend towards thicker moss and organic mats. However, these stands rarely occur where organic matter accumulation exceeds 25 cm (field observ.). Viereck (1970), in a comparison of the thermal regime of four river bottom stands in central Alaska, concluded that soil temperatures can be related to soil textures and thickness of the insulating mat. Fall freezing and spring thawing were slower in the finer-textured soils, in part because these soils retain more water, and therefore evolve more latent heat of fusion (Geiger 1965). Sand underlying *Salix alaxensis* froze to 150 cm depth in two months; balsam poplar and white spruce communities on silt and sand froze in three months; in the white spruce--black spruce/shrub/feather moss community with a 27 cm thick moss/organic layer over silt and sand, hard freezing at only 50 cm depth did not take place until 16 February, four months after the surface began freezing. Spring thaw began in late May and was never completed on the finer-textured soil with thick organic mat,

while on sand with scattered *Salix alaxensis* and a loose low moss mat, thawing was complete by the end of May. Soil temperature fluctuations were greatest in the sandy willow stand and lowest in the spruce communities. While dry coarse-textured upland soils with a thin organic layer are warmer during summer, they cool rapidly to freezing in the fall, depriving plants of liquid water and bringing about a sharp drop in metabolism at a time when dormancy--hardening processes may be incomplete.

The available data indicate that adult trees are fully capable of survival and growth, albeit slow, at their high subarctic distribution limits. While growing conditions for adult trees are not conducive to rapid growth on wet and summer-cold soils, conditions for seed reproduction and cloning seem favorable.

The treelessness of dry soils at the southern limit of the forest-tundra may result from physiological stresses to seedlings during germination and establishment, brought on by droughty conditions, wide fluctuations in soil temperatures, and perhaps to inadequate snow cover. Such conditions might manifest themselves in poor resistance to frost and desiccation. Year-round meteorological, physiological, fire, and soil studies in these stands are needed before landscape patterns of trees and tundras at their distributional limits are understood.

5.4 Areal pattern of burn in the subarctic NWT

Fire occurrence and behavior and vegetation regeneration rate are discussed as a basis for interpreting the areal pattern of burned forest and forest-tundra. The complex areal pattern of burn in the subarctic NWT is understandable with reference to weather, terrain influences, and regeneration rates.

5.4.1 Factors affecting fire occurrence and behavior

Fuel, topography, and weather all influence fire occurrence and behavior. Closed crown forest carries fire better than open crown forest or treeless vegetation. In tundra and forest-tundra, fires are carried by continuous, fine-textured ground vegetation rather than by tree crowns. Smooth terrains, with continuous mature forest and a low areal cover of water bodies, appear most susceptible to large burns. Lightning discharged during summer thunderstorms is the primary cause of fires in the subarctic NWT.

Fuel, topography, and weather all influence fire occurrence (frequency). A deep accumulation of dry fine fuels and duff such as conifer needles, twigs and lichens, and dry dead trees favor fire spread (Simard 1973; Bradley et al. 1982). Since fruticose lichens such as *Alectoria*, *Cladonia*, and *Stereocaulon* dry rapidly and

have high surface to volume ratios, they behave more like fine litter than living vascular plants (Auclair 1983), and are thus fire-prone. Squirrel middens at the bases of trees and accumulations of arboreal lichens both encourage intense fires (Rowe 1970; Larsen 1980). Probability of fire increases with age of tree stands due both to buildup of stand biomass and establishment of a closed lichen mat (Rowe et al. 1975; Auclair 1983).

Continuity of the fuel favors fire spread; closed crown forest carries fire better than open crown forest or treeless vegetation (Bradley et al. 1982). In tundra and forest-tundra, fires are carried by continuous, fine-textured ground vegetation rather than by tree crowns (Wein 1975). Communities with a high cover of resinous evergreen shrubs ignite at low temperatures and can burn intensely as those shrubs have high lipid and caloric contents (Auclair 1983). Once ignited, dwarf birch--ericad/lichen vegetation burns fiercely (Crampton 1974). Dwarf willow--birch, cottongrass, and even sedge meadows have been known to burn (Wein 1976). Plants with high ash contents such as graminoids are less flammable than resinous shrubs (Auclair 1983).

Topography affects both rate of fire spread and extent of burn. Smooth terrains encourage and rough terrains discourage large fires (Simard 1973). Moist floodplain forests are relatively fire-proof (Rowe et al. 1974); whereas coarse soils over bedrock dry quickly, making such sites more fire-prone than those on deeper fine-textured soils (Bradley et al. 1982). Thus the extensive terrains with coarse-textured shallow soils north of Great Slave Lake and south of the East Arm of Great Slave Lake are fire-prone landscapes. In contrast, sparsely-forested rocky uplands set in a matrix of barren

rockland present discontinuous fuels and are thus less fire-prone than continuous forest (Rowe et al. 1974).

Lakes larger than 15-20 km² are evidently effective firebreaks. Airphoto analyses and study of fire cover maps indicates that burns are commonly halted at large bodies of water. Kelsall (1960), working north of Great Slave Lake, listed rain, old burns, lakes, streams, and bogs as significant controls to burning. Terrain with a high cover of water appears to be less fire-prone than lake-free terrain.

While variation in fuel and topography result in changes in fire behavior of no more than a factor of 10, weather can cause fire behavior to vary by a factor of 1000 (Simard 1973). Lightning discharged during summer thunderstorms is the primary cause of fires in the subarctic and boreal NWT. Rowe et al. (1975) found that lightning accounted for >97% of the total area burned in the Yellowknife district since 1970. Elsewhere in the western NWT, lightning accounted for >99% of the area burned. Johnson and Rowe (1975) determined that 85% of fires in the Caribou Range SE of Great Slave Lake were caused by lightning and 15% were caused by man; 99.9% of the total area burned was due to lightning.

Lightning requires air mass instability due either to orographic effects, frontal movements, or convective instability (Rowe et al. 1975). Of the three sources of air mass instability, convection appears to be the prime cause of lightning in the western NWT (Rowe et al. 1975). Once ignited, fire spread is favored by low relative humidity and high winds (Cochrane and Rowe 1969).

5.4.2 Recovery time after fire

The balance between yearly burn and recovery time determines the landscape cover of "recent" burn. Regeneration of low subarctic tree stands beyond the shrub stage generally takes place within 25-50 years after fire. Forest-tundra tree stands are, in comparison to low subarctic forests, fire-proof. Black spruce is apparently better adapted to fire than white spruce and larch. The forest-tundra of the northwest may be susceptible to rapid shifts in position as white spruce is by far the dominant tree.

Regeneration after fire must be considered along with fire occurrence as the balance between recovery time and yearly burn determines the landscape cover of "recent" burn. There is general consensus that recovery of burned subarctic tree communities requires ever greater lengths of time as the limit of trees is approached, but hard data are lacking. Many papers nominally reporting on the role of fire in the forest-tundra contain a minimum of evidence, and instead report on the low subarctic (cf. Kershaw et al. 1975; Kershaw and Rouse 1976; Auclair 1983).

Recovery in low arctic tundra is rapid in comparison to that in low subarctic tree stands because tundras accumulate less combustible biomass and are frequently underlain by cold wet soils resulting in cooler fires (Bliss and Wein 1972). In tundra, therefore, many underground parts are undamaged by fire, making regrowth possible during the same or next growing season (Wein 1975). Tundra fires may be more common than previously thought; rapid regeneration can make

identification of past burns difficult within only a few years of recovery (Cochrane and Rowe 1969).

Study of airphotos taken in different years in the northwest indicates that upland tundra burns are not uncommon. Tundra burns are evidently less frequent elsewhere in the high subarctic (Wein 1976; field observ.). During the fieldwork we observed past burns in peat plateaus and other dry peats, and only a few examples of burned sparsely-treed uplands in a tundra matrix. The total cover of burned tundra communities in the high subarctic may be estimated as $<0.01\%$ (field observ.). Tundra fires in Keewatin may be less rare (Wein 1976).

Recovery times for tree vegetation differ geographically, by community type, and depend also on definition criteria. Regeneration of low subarctic tree stands beyond the shrub stage generally takes place within 25-50 years after fire (Kershaw et al. 1975; Wein 1975; Johnson and Rowe 1977). In the low subarctic Caribou Range SE of Great Slave Lake, recovery of black spruce on drumlins takes place in about 50-60 years, but climax is not reached until about 200 years (Kershaw et al. 1975). High canopy cover in the Caribou Range is reached within 50 years in various forest types (Johnson and Rowe 1977). In general, canopy cover of mature forest in the Caribou Range is lower than that of seral stages. Stand thinning is especially notable in sites supporting paper birch since clones senesce at about 50 years (Johnson and Rowe 1977). On sites with adequate moisture, the seral spruce/*Stereocaulon* woodlands are replaced by closed canopy climax spruce/moss forests after about 150 years (Kershaw and Rouse 1976).

In the northwest, burned tree stands in the lower Mackenzie valley may remain shrub-dominated for 25-50 or more years after fire; such stands may require 50-120 years before the community appears stable (Wein 1975; Black and Bliss 1978). Black spruce/*Vaccinium uliginosum*/lichen climax forest there may require over 200 years to reach maturity; the persistence of a shrub-dominated stage may be due to improved water and nutrient availability on fine-textured tills resulting in luxuriant growth (Black and Bliss 1978). Stand thinning takes place with age in the northwest as a result of rise of the permafrost table. This thinning is most striking when viewed from the air, as the dark-toned spruce, shrubs, and moss are frequently restricted to runnels which contrast with the light-toned *Cladonia* dominated interfluves.

By virtue of their isolation and often moist soils, forest-tundra tree stands are, in comparison to low subarctic forests, fire-proof. Mature stands are usually uneven-aged, indicating good recruitment, and older trees often exceed 200-250 years of age (field data). If these stands are burned, however, their recovery is uncertain (Rowe 1970; Payette and Gagnon 1985) (Plate 12).

Spruce are apparently unable to sprout from underground parts after fire, at least in the low subarctic (Johnson and Rowe 1977); regeneration thus begins with re-seeding. Black spruce, which produces cones at an earlier age and retains some unopened cones on the tree, is better adapted to fire than white spruce and larch, which shed more of their total seed crop each season (Rowe 1970; Payette et al. 1982). But seeding from cones retained on fire-killed black spruce must take place within 1-8 years after fire as the seeds lose their viability

with time (Black 1977). Buried black spruce and larch seed populations in the subarctic are evidently non-viable (Johnson 1975; Black 1977; Payette et al. 1982), making re-seeding of burned areas from within a stand subject to time constraints. The nearly complete non-viability of buried seeds, compared to the relatively high seedling populations in larch and black spruce stands in northern interior Québec, indicates that northern tree stands may be renewed by a seedling bank (dating from episodic establishment) rather than from a seed bank (Payette et al. 1982). Such stands are at risk of extinction by fire unless the fire is sufficiently patchy to allow survival of some seedlings. Seeding from outside the burn is subject to the vagaries of isolation, patch or "island" size, viable seed production, dispersal, and successful establishment. Although fires are rare in the forest-tundra, tardy or unsuccessful regeneration might locally shift the tree limit south of its climatic potential (Rowe 1970), or more precisely, south of the climatic potential of adult trees.

In contrast to rapid regeneration after tundra fire, burned tree stands near their polar limits can be converted into persistent "tundra" communities. The potential for post-fire tree regeneration in the forest-tundra of northern Québec may depend on (1) the regeneration potential of the stand: either forest trees (bearing normal cones) or clonal spruce (with stunted spruce bearing only a few small cones, sometimes none); (2) on the length of fire intervals; and (3) on the timing of fire occurrence in relation to climatic conditions (Payette and Gagnon 1985).

White spruce stands lack a supply of stored seeds, and thus fires near tree limit could result in conversion to "tundra". The

forest-tundra of the northwest may be susceptible to rapid and persistent depression of potential tree cover as white spruce is by far the dominant tree. Rowe (in Rowe and Scotter 1973) has observed fire-induced "tundra" in the Horn Plateau near Ft. Simpson, NWT. Similar fire-induced "tundras" have been observed in northern Manitoba (Ritchie 1960a), northern Québec (Payette 1983; Payette and Gagnon 1985), Fennoscandia (Hustich 1966), and elsewhere across the circumpolar subarctic.

5.4.3 Patterns of fire occurrence and burned landscape in the subarctic

Burns show a general decrease in cover from the far northwest to the southeast, while cover of water bodies increases from northwest to southeast. The role of lakes acting as firebreaks or in locally modifying summer weather deserves further attention. In the northwest, the uniformity of the flat till plains, high cover of mature forest, and scarcity of lakes, coupled with dominance of white spruce (in the forest-tundra), are likely primary factors accounting for the extensive burned terrain. In the eastern half of the study region, tree cover usually drops rapidly within the southern half of the forest-tundra, constraining burn to low cover values; burns extend about 25-75 km into the forest-tundra, reaching ever lower cover values with distance east of Great Slave Lake. Low fire weather risk and an abundance of lakes, coupled with the typical steep drop in tree cover, may account for the low cover of treeless burn both in the open crown and forest-tundra

regions east of Great Slave Lake. Treeless burns north of Great Slave Lake peak in cover in the low subarctic along a NW--SE axis which lies NE of high fire risk and occurrence zones.

Average fire occurrence for the high subarctic ranges from nearly zero at the limit of trees to >0.6 fires/1000 km²/year near the southern edge of the forest-tundra (Rowe et al. 1975; Simard 1975). Highest fire occurrence is found in the low subarctic and high boreal regions north of Great Slave Lake (about 1.5-4 fires/1000 km²/year), extending from near Lac La Martre SE to Yellowknife (Simard 1975). Fire occurrence decreases sharply to the SW, but remains high well to the NE on the Shield, averaging 0.2-0.8 fires/1000 km²/year in the low subarctic north of Yellowknife, and 0-0.4 fires/1000 km²/year in the forest-tundra (Simard 1975). A similar zone of high fire occurrence lies south and SE of the East Arm of Great Slave Lake (0.2-0.8 fires/1000 km²/year).

A high fire risk zone along the western edge of the Shield NW of Yellowknife has been identified by Rowe et al. (1975). There low pressure systems moving south up the Mackenzie valley apparently interact with high pressure systems moving SE parallel to treeline. The Arctic and Pacific highs which collide near the southern edge of the forest-tundra in summer are separated by a trough of low pressure (Rowe et al. 1975). The interaction of these high and low pressure systems causes mixing of warm southern air with cool northern air; airmass instability is created, resulting in thunderstorms and lightning.

Fire weather zones (based on empirical relationships between lightning, rainfall, wind, humidity and other indices with fire behavior) identified by Simard (1973) run nearly parallel to the forest-tundra from the Mackenzie valley to the East Arm of Great Slave Lake. East of Great Slave Lake, fire weather zones trend more north-south than do the vegetation zones, indicating that the eastern forest-tundra is less fire-prone than that north of Great Slave Lake. Perhaps contrary to expectations, weather presents low to very low fire risk in the northwest (fire weather index of 2-6; Simard 1973), although treeless burns there reach their highest cover in the study region. Moderate to high fire risk (FWI 6-14) exists for the sector between Great Bear and Great Slave Lakes, and moderate fire risk (FWI 6-10) exists from the East Arm of Great Slave Lake to the Manitoba--Saskatchewan border at 60° N. In the subarctic of southern Keewatin and northern Manitoba, fire risk is low to very low (FWI 2-6; Simard 1973).

The areal pattern of burn cover (Figure 18) may be divided into three sub-regions: the northwest, extending SE to the south shore of Great Bear Lake; the central third, lying between Great Bear and Great Slave Lakes; and the southeast, extending from the East Arm of Great Slave Lake to Hudson Bay.

Treeless burns reach their highest cover and greatest extent in the northwest. In the high boreal and low subarctic of the northwest, 10-50% of the terrain is treeless due to burn. In the forest-tundra, burn area varies between 0-25%, with the northern limit of burn nearly reaching the limit of trees between the Mackenzie and Kugaluk Rivers.

The northern limit of burned trees reaches the big bend of the Anderson River, then parallels the Anderson southward to Smith Arm of Great Bear Lake. Peaks of >25% burn are found in the Colville Lakes area SW of the Anderson. Extensive burns are found in the flat terrain west of Keith Arm, and burn cover remains high along the south shore of Great Bear Lake eastward to the Shield/Paleozoic border (10-50%).

As noted above, weather presents low to very low fire risk in the northwest (Simard 1973), and cannot account for the observed high cover of treeless burns. The continuity of the forests, particularly black spruce/heath shrub/lichen, and the maturing of vegetation not burned since the 1800's have been suggested as contributing to the great extent of burns in the northwest (Rowe et al. 1974; Black 1977). In addition, large fires are favored by the topographic uniformity of the extensive flat till plains, and by the scarcity of lakes which might act as firebreaks (see Wein 1975: Figure 1). Comparison of Figure 8 (percent water) and Figure 18 (percent burned trees) indicates that the most extensive burned terrain is found where cover of water bodies is lowest (0 to <10%). Fires may spread unhindered across the relatively lake-free till plains of the northwest.

The western forest-tundra pattern, in which tree cover may remain high to near the limit of trees (Figure 23B), contributes to high burn cover by providing relatively continuous flammable vegetation. In addition, white spruce, stands of which lack a supply of stored seeds, is the dominant tree in the forest-tundra of the northwest and apparently regenerates poorly after fire near its northern limit.

In the eastern half of the study region, tree cover usually drops rapidly within the southern half of the forest-tundra, constraining

burn to low cover values (Figures 18, 24, 25). Burns extend into the forest-tundra a distance of about 25-75 km. In general, the northern burn limit does not extend beyond the line where tree cover equals upland tundra cover (the central line in Figure 24B.1).

Between Great Bear Lake and the East Arm of Great Slave Lake, forest-tundra burn cover ranges from 0-10%. There is a band of high burn cover (10-50%) NE of the Shield/Paleozoic border in the low subarctic, falling off both to NE (forest-tundra) and to SW (high boreal). Based on low-level aerial surveys in the low subarctic Camsell--Hardisty--Indin Lakes area in this central region, Kelsall (1960) calculated burned forest cover at 22% of the landscape.

Corroboration of this band of high cover of burn is provided by inspection of fire maps (DIAND, NWT govt., unpublished, supplied by Dr. Kaye MacInnes) of the area north and NW of Yellowknife. For the area lying between 116 and 114°W and 62 and 66°N, high cover of fresh burn occupies a band lying between 62° 50' and 64° 25'N. Farther west, in the Lac La Martre--Faber Lake area, percent cover of burn peaks to the NE, with low cover of burn south and west of Faber Lake.

Maps of fire weather and fire occurrence (Simard 1973, 1975), burn cover (DIAND, NWT Govt, unpublished; Kelsall 1960), and the fire risk zone of Rowe et al. (1975) parallel the band of high cover of burned trees lying NW of Yellowknife. High fire occurrence and risk evidently occupies a band SW of the peak burn cover in Figure 18. The discrepancy between Figure 18 and other accounts may reflect the offsetting factors of high fire occurrence southward and longer recovery time northward. The balance between yearly burn and recovery

time determines the amount of the landscape currently treeless due to burn.

Burn cover in the forest-tundra north of Great Slave Lake (0-10%) generally exceeds that east of Great Slave Lake (0-5%). Aside from the factors of higher fire occurrence and fire risk, a third factor may be cover of water bodies (cf. Figure 8 (percent water) and Figure 18 (percent burn)). Water bodies cover 10-25% of the forest-tundra north of Great Slave, averaging about 15%. In contrast, water cover east of Great Slave Lake ranges between 10-50%, with an average near 20%.

In the low subarctic Caribou Range (south and SE of Great Slave Lake), burn cover peaks (50%) where water cover reaches a minimum ($\leq 10\%$). In contrast, the forest-tundra SE and east of Great Slave Lake is comparatively burn-free; only 0-5% of the terrain is treeless due to burn. Like the area north of Great Slave, burns extend about 25-75 km into the forest-tundra east of Great Slave, but average burn cover is lower and the limit of burns lies generally closer to the southern edge of the forest-tundra. In the extreme southeast, burn cover in the low subarctic of northern Manitoba rises (up to 25%); here water bodies cover only 2-10% of the landscape.

5.5 The sigmoid cover structure of the forest-tundra in relation to environmental factors

The sigmoid cover structure of the forest-tundra may be viewed as the integrated response of the vegetation in its attempt to track environmental variability: a summation of vegetation response, edaphic

influences, fire patterns, and landscape--climate feedbacks.

The structure (in this sense: treeless, clonal, and forest sites) of the modern forest-tundra zone may be "...the result of long-term regeneration dynamically related to Holocene climatic changes and to fire history." (Payette and Gagnon 1985:572; see also Payette 1983; Millet and Payette 1987). Accordingly, the forest-tundra is seen as the result of Holocene deforestation of a formerly densely forested zone effected by fire under an unfavorable climate. "Tundra" thus owes its origin to failure of tree regeneration after deforestation.

Alternately, the sigmoid cover structure of the forest-tundra might result from bioclimatic feedbacks (bounded by the maximum and minimum radiant energy available to the region and the limits to areal cover of trees or tundra: 0--95%), edaphic factors, fire patterns, and vegetation response times (sections 5.2.3, 5.2.4.2, 5.4). Hypothesized controls of zonal vegetation structure, in space and time, are outlined in Figure 28.

Climate is linked with the landscape through terrain features such as albedo, aerodynamic roughness, and depth and duration of snowcover, with this linkage strongest at the local micro- and mesoclimatic level. Influence upon climate at the regional level may take place through air mass modification and effects upon circulation patterns.

Since terrain features affect air mass characteristics, steep gradients in upland tundra or tree cover should be correlated with steep climatic gradients. As discussed in section 5.2.2, this is roughly corroborated by vegetation--climate comparisons.

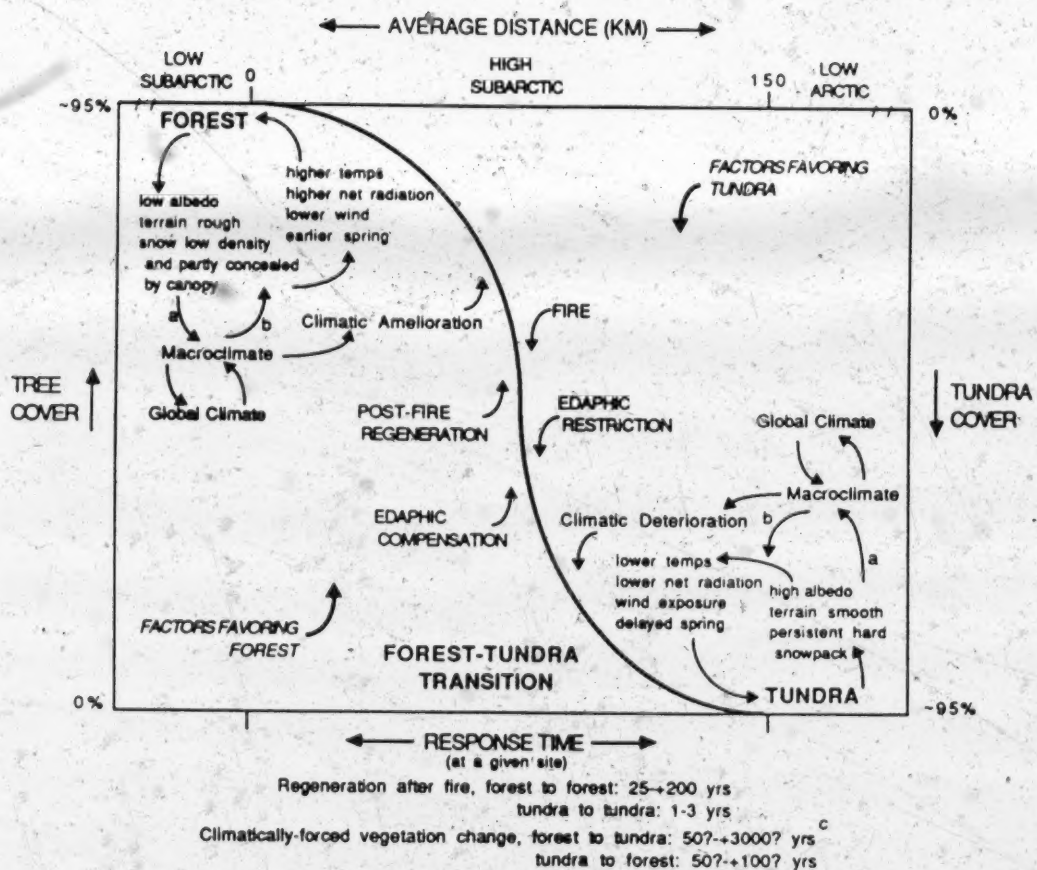


Figure 28. Hypothesized vegetation, climate, snowcover, fire, and edaphic relationships functioning across the subarctic forest-tundra. Post-fire regeneration rates are based upon sources listed in section 5.4.2, and response times to climatic change upon sources in section 5.1. Footnotes: a = air mass modification, effects upon circulation patterns; b = macroclimatic constraints upon meso- and microclimate; c = fire may immediately convert forest (persisting under a tundra climate) into treeless vegetation.

Tundra communities with their shorter plants are covered by snow for 8-9 months of the year; any plants projecting above the snowpack risk physical injury from snow crystals blown about by the unabated winds of the tundra. These smooth, snow-covered communities thus reflect most of the sun's energy back to the atmosphere, radiation that could otherwise warm the landscape. In summer, albedo differences between vegetation zones are not appreciably different, but vary from site to site with differences in vegetation tone, surface roughness, and soil moisture. Typical summer albedos are 15-26% for tundra; 16-22% for forest-tundra; and 11-19% for open crown forest (Davies 1966; Hare and Ritchie 1972; Haag and Bliss 1974; Findlay and Treidl 1975; Petzold and Rencz 1975; Rouse 1976), with highest values for lichen-rich tundras (Davies 1966; Petzold and Rencz 1975).

In contrast, winter albedos vary with differing exposure of snowcover from 70-80% in tundra; 60-67% in forest-tundra; and 50-55% in open crown forest (Hare and Ritchie 1972; Findlay and Treidl 1975). Fall and spring values are intermediate, but the large albedo differences of winter persist well into the high insolation period such that spring is delayed by long-lasting snowcover (Hare and Ritchie 1972). For example: (1) small lakes in the Inuvik area are ice-free by mid-June, but ice-out does not occur till the first week of July near Tuktoyaktuk, only 150 km northward (Ritchie 1977); (2) an estimated 600% increase in absorbed radiation at the surface took place after a rapid disappearance of snow from the Keewatin tundra in June 1963 (McFadden 1965); (3) through its combined effects on albedo, soil insulation, and evaporation, a one month delay in disappearance of snowcover has been estimated to decrease summer monthly temperatures by

8.6 C (June), 8.8 C (July), and 3.4 C (August (Lettau and Lettau 1975)).

Frozen snow-covered lakes have high albedos typical of tundra in winter. McFadden (1965) reported albedos of 70-92% for frozen snow-covered lakes in the tundra of central Canada, and 30-68% for similar lakes in the forest. In contrast, an ice-free lake might have an albedo of 8-12.5%. When lakes are partially frozen, with no snow on the surrounding landscape, typically in spring, lakes increase the local albedo (McFadden 1965). The lake effect on albedo is greater in the forest than in tundra as the frozen and snow-covered lakes contrast with dark forest canopy; in winter these lakes may raise the average albedo of an area by a factor of two as compared to forested areas without lakes and bogs (McFadden 1965). Thus forest-tundra landscapes with a high cover of lakes may have climates more typical of tundra than forest.

The transition from forest to tundra (or treeless surfaces) contributes to the severity of the climate (Hare and Ritchie 1972), inducing a further reduction in tree cover. Conversely, tree planting in the southern tundra of the USSR is believed responsible for climatic amelioration (Tikhomirov 1961), although careful study of this effect is required to account for independent climatic trends. Climate--vegetation feedbacks have also been implicated in intensifying the effects of the Sahelian drought of 1968-73, and, in the desertification of sub-tropical semi-arid regions since mid-Holocene times (Hare 1979).

In the steep phase of the vegetation cover gradient, positive feedbacks between vegetation, climate, and snowcover may drive the

landscape to either forest or tundra dominance. Maximum winter surface albedo illustrates the point. Between 90 and 100°W, maximum surface albedo increases from about 40% in the closed crown boreal region at 56°N, to about 78% by 63°N, thereafter remaining stable into the high arctic (Robinson and Kukla 1985).

At high and low cover values, where tree or tundra vegetation occupy <5% of the landscape, vegetation gradients flatten out and trees or tundra can be found far to the north or south on favorable sites. The primary controls of tree and tundra cover at the extremes of the forest-tundra appear to be topoclimatic and edaphic, but bioclimatic feedback and historical factors may also be influential. Upland tundra at its southern distribution limits typically occupies coarse-textured dry soils, exposed summits, and highlands. Conversely, trees at their polar limits are usually restricted to wet or wet-mesic mineral soils, often lining small drainages. In the northwest, northern Manitoba, northern Québec, and elsewhere, fire has created pseudo-tundras which owe their existence to failure of tree regeneration.

An analagous situation may exist in the prairie--deciduous forest ecotone of the Upper Midwest, USA: Davis (1977) concluded that the position of the ecotone is attributable to climatic controls, with local variation in character conditioned largely by edaphic factors, topography, fire, differential migration rates of some taxa, and survival of relicts in favorable habitats.

Vegetation--climate--snowcover feedbacks were first postulated in 1972 by Hare and Ritchie. They hypothesized that the zonal divisions of the boreal forest are a series of interlocking systems of vegetation and climate, and not a simple expression of climatic control over

vegetation. The results of this quantitative study of forest-tundra vegetation provide evidence in support of the interlocking nature of vegetation and climate. It is likely that nothing short of an integrated system of climate and landscape could account for the observed consistent patterns of vegetation cover across the forest-tundra (synthesized in Figure 28).

Differences in the vegetation cover pattern (i.e., variation in the form of the sigmoid curve) may arise through topoclimatic, edaphic, and fire influences, human disturbance, and by the response time of the vegetation (Figure 28). It is noteworthy that the symmetry of the sigmoid cover structure of trees is diminished when burned (but potentially forested) terrain is not summed with terrain currently forested. The pattern might then be better described by a truncated sine wave due to depression of potential tree cover in the southern forest-tundra.

Forest bioclimatic feedbacks, rapid post-fire regeneration, and edaphic compensation might act to maximize tree cover in space or time, resulting in a steep cover gradient at the climatic threshold for tree growth. Tundra bioclimatic feedbacks, deforestation, and edaphic restrictions, in contrast, might act to limit forest growth in space or time; steep gradients would occur south of the climatic potential for trees, resulting in a broad (spatial) or persistent (temporal) tundra-dominated zone and a narrow or transient forest-dominated zone.

Edaphic controls and fire effects are exerted most strongly at the individual plant, vegetation stand, and vegetation subtype scales (10^0 - 10^6 m²; see Delcourt et al. 1983) which, in aggregate, might influence the vegetation structure of the forest-tundra macroscale

(10^{12} m^2). Bioclimatic effects are felt at all scales, from local (10^0 - 10^6 m^2) and area (10^6 - 10^9 m^2) microclimatic and mesoclimatic influences, to the regional macroscale (10^9 - 10^{12} m^2), with commensurate effects upon the macroclimate.

Response rates of forest-tundra vegetation vary widely. Regeneration of burned tundra to a stage that would be undetectable on airphotos may require only 1-3 yrs (section 5.4). In contrast, burned tree stands require a minimum of 25-50 yrs to achieve a treed condition, and may require +200 yrs to reach a stable condition; burned tree stands may remain treeless indefinitely under an unfavorable climate.

Rates of climatically-forced vegetation change are likely more rapid from tundra to forest than from forest to tundra (section 5.1; Bradley 1985:267). As rough approximations requiring quantification of both climatic stimulus and vegetation response, a tundra to forest succession at a given site might take place in 50-100 yrs; in contrast with a forest to tundra succession (unaccelerated by fire) which might require 50-+3000 yrs. As indicated by the more rapid tundra to forest succession, the processes involved may be fundamentally different. A tundra is converted to a forest stand by tree establishment and reproduction in a relatively open habitat. A forest is converted to tundra by death of individual trees and clones, resulting in opening of the stand. In the absence of fire, trees might persist through unfavorable periods, adding little or no biomass, and produce new cohorts during a climatically favorable episode.

Climatic variation (change) -- of differing magnitude, duration, central tendency, and variability (Hare 1979) -- favoring opposing

vegetation responses of unequal rate, must create an exceedingly complex mosaic in both space and time. In the absence of fire, afforestation is probably more rapid than deforestation; on average, therefore, the forest-tundra should support more tree vegetation than the current climate sanctions. The overall effect of fire should be to bring the balance between tree and tundra vegetation closer to equilibrium with climate. Since, in an absolute sense, climate is never constant (see Hare 1979; Bradley 1985; Woodward 1987), and vegetation response lags, it might be argued that forest-tundra vegetation cover never achieves complete equilibrium with climate. The sigmoid cover structure of the forest-tundra might be viewed as the integral of the vegetation's response in its attempt to track environmental variability: a summation of vegetation response, edaphic influences, fire patterns, and landscape--climate feedbacks.

Studies of vegetation response times, due to climatic forcing, fire, or human disturbances, are sorely needed (see Delcourt et al. 1983; Woodward 1987), especially in the north (e.g., Payette and Gagnon 1985; Millet and Payette 1987). Significant changes in the vegetation cover of the subarctic may be taking place currently. If there is a lag of ~50-100 yrs in afforestation response, current tree cover may be increasing in response to the warmth of the early 20th century (even though the recent post-1940 trend of atmospheric and sea-surface temperatures for the northern hemisphere has been downward at 0.1-0.2 C/decade (Hare 1979)). If there are significant increases in tree density and consolidation of forest stands, might bioclimatic feedback interact with greenhouse effects to provide further momentum for

vegetation change? How might future climatic warming affect fire patterns? Large wildfires in the southern forest-tundra might increase the frequency of deforestation such that forest cover might decrease there, while disjunct, relatively fire-proof tree stands in the northern forest-tundra undergo net expansion (see Payette and Gagnon 1985).

5.6 Needs for further research

The time is now to assess what, if any, changes are taking place in the forest-tundra vegetation cover. The maps presented in this work provide a baseline for vegetation conditions that prevailed circa 1960. In a sense, the maps may be already out of date, yet this may prove an asset in determining the degree of vegetation change over a finite time. In this regard, studies of population and areal cover dynamics might prove fruitful in the forest-tundra east of Great Slave Lake. There, the landscape is "primed" for afforestation: steep vegetation change takes place in the southern forest-tundra, with low tree cover extending great distances northward; increase in forest cover might be readily detectable. In contrast, much of the northwest forest-tundra supports high tree cover to near the limit of trees, and detectable expansion might require establishment of new populations; furthermore, northward movement of the vegetation zones is constrained by proximity to the Arctic Ocean. On the other hand, studies of tree regeneration in the persistent dwarf birch--willow--alder treeless burns of the northwest may prove enlightening.

This study has attempted to describe the vegetation cover of the high subarctic forest-tundra, and discussed the likely controls and correlates of the vegetation patterns. In my opinion, the location of the forest-tundra boundaries, the distribution of selected patterned ground features, vegetation pattern and gradients within the forest-tundra, and the sigmoid cover structure described in this study rest on firm empirical ground. Explanations for many of these patterns, however, will require interdisciplinary research and hypothesis testing. Suggestions for further research are outlined below.

5.6.1 Bioclimate

To assess the effects of vegetation structure and snowcover on microclimate and mesoclimate, an intensive comparison of contiguous, topographically uniform areas (thereby holding macroclimate and site influences constant) should be undertaken. At 3-4 sites, the following parameters could be monitored: incoming global solar radiation, albedo, absorbed solar and net radiation; temperature at screen level, ground surface, and below-ground; snow depth, density, and decay over time; wind speed profiles. Simultaneous phenology (time of bud break, leaf expansion, elongation) and physiology (metabolic rates, onset of dormancy) studies would complement the meteorological data. The vegetation--climate--snowcover relationships shown for a small geographic area should apply to the landscape at large.

Climatic anomalies apparent between the forest-tundra of the northwest and the southeast (sections 5.2.4, 5.2.4.1) require verification. A simultaneous study to assess the parameters given above should be undertaken in two strategic areas. Vegetation communities in the two widely separated areas (northwest vs. southeast) should be as identical in structure as possible. Ideally the study would (1) extend over a transect of ~100 km (rather than a single site) and cross identical vegetation cover isolines (e.g, spanning the 10:1 to 1:10 transition of tree:upland tundra cover ratio); and (2) be conducted across terrain that is typical of the region. A third transect north of Great Slave Lake would test the validity of the vegetation--climate crossover zone, and would provide a transition between the northwest and southeast transects.

Another study might be conducted in the vicinity of the major tree stands along the middle Thelon River (or its tributaries). Comparison of the mesoclimate of the valley with that of the tundra plain would determine whether the Thelon valley is a thermal oasis.

5.6.2 Edaphic controls

Edaphic effects on tree species distribution should be studied both under controlled environment and field conditions. Spruce and larch seeds and seedlings of known forest-tundra provenance should be collected and grown under controlled conditions. During collection, care should be taken to ensure sufficient numbers of viable seeds (see Payette et al. 1982). Soil media should be prepared to approximate

average northwest or southeast soils in terms of texture, nutrient levels, pH, and CEC (see section 4.4).

Northwest plants should be grown on typical home provenance northwest-type soils, and for comparison, on southeast-type soils; the same cross-comparison should be done for southeast plants; some plants from both provenances should be grown on control media. Seed viability, germination, and growth over a range of temperatures and soil moistures should be assessed. Germlings and seedlings could be subjected to water and thermal stress to assess survival. These growth trials would provide a test of soil factors on survival and growth of juvenile spruce and larch, and possibly indicate ecotypic variation.

In the field, tree stands at their northern limits (or, tundra stands at their southern limits) could be studied. Contiguous tree stands of equal age, differing only in soil and/or snowcover conditions should be chosen. Stand population data (number of cones/tree, seeds/cone, seed viability; seedling, sapling, and tree density; vegetative vs. sexual reproduction, vigor, growth rates; and phenology) could be compared between stands. Soil nutrient regime, water potentials, temperature, depth to permafrost, and snow parameters should be compared between stands. A transect through a transition from a forest to tundra along a soil catena could be run, comparing tree population parameters with soil and snowcover conditions. Informative comparison of forest-tundra stands could be made in the vegetation--climate--terrain crossover region north of Great Slave Lake. In the vicinity of Point Lake, e.g., tree and tundra stands growing on a variety of parent materials should be locatable.

5.6.3 Cover structure

Study of the underlying reasons for the sigmoid cover structure of the forest-tundra of the NWT presents difficulties. The structure may depend as much on past environmental conditions as it does on the present. Results from studies of bioclimate (5.6.1) and edaphic controls (5.6.2) may shed some light on the problem, but reconstruction of paleo- and recent climate and fire regimes will also be required. Study of vegetation response times is critical: dendroclimatology and study of tree population structure, tied to independent, high resolution climatic records, might permit calibration of climatic event with vegetation response. It would be interesting to know, e.g., whether six years of summer temps 0.5 C above average have the same effect on vegetation as three years of summer temps 1 C above average.

Improvements in remote sensing technology may permit resolution of fine details in vegetation cover. If so, similar subarctic vegetation cover contour maps and diagrams could be produced and compared with those presented in this study. Comparison of cover--time sequences might indicate changes in vegetation cover traceable to known events.

6 CONCLUSIONS

6.1 Relicts, treeline history, and the eastern forest-tundra

Although tree stands at their northern limits in the forest-tundra east of Great Slave Lake have been widely considered to be relictual, northern forest-tundra "outliers" there lie climatically well south of most of the forest-tundra of the northwest. The great breadth of the eastern forest-tundra is thus viewed as the result of the persistence, on a grand scale, of tree stands left behind by a southward retreating mid-Holocene forest. Such northern stands, seen as lacking the sanction of the present climate, may lack regular sexual reproduction.

There are two main difficulties with this view, stemming from (a) the problem of interpretation of paleoecological data; and (b) the question of what constitutes "relict" vegetation.

6.1.1 Interpretation of forest-tundra paleoecological data

Difficulties in reconstructing past vegetation and climate are: identification of a forest-tundra pollen spectrum; important yet "palynologically silent" taxa; the extrapolation of locally valid results to regional status; and interpretation of paleosol and charcoal evidence and changes in spruce pollen influx. Evidence for Holocene treeline migrations in the NWT is equivocal,

difficult to generalize to regional status, and may be interpreted more parsimoniously in terms of climatically induced changes in pollen production, tree density, and consolidation of pre-existing stands.

6.1.2 Relict vs. dynamic forest-tundra vegetation

Period of establishment of northern forest-tundra tree stands, inferred from paleobotanical data on former extent of forest, is estimated as mid-Holocene (circa 6000-3500 BP). Although some northern sites may have been treed more or less continually since the mid-Holocene, perhaps periodically disturbed by fire or minor climatic oscillations, such relict stands have never yet been identified.

Relatively young clones and single-stemmed spruce stands, that have established since 1850 A.D., are common in the northern forest-tundra: in the Mackenzie District; near Churchill, Manitoba; and in northern Québec. Recent establishment of trees in the northern forest-tundra of the USSR has been noted. Elevations of subalpine timberlines have risen in most parts of the boreal USSR in this century in response to recent climatic amelioration, as has also been documented for the mountains of Fennoscandia and Alaska. Far from being relictual or historical, it appears that many subarctic and subalpine trees at their distributional limits are newly-established.

The vegetation pattern of tree stands "north" and tundra stands

"south" of a core of steep cover gradients is as fundamental a characteristic of the forest-tundra as the treeline itself. Northern forest-tundra vegetation might be better viewed as dynamic in space and time.

6.2 Vegetation, climate, and terrain relationships

6.2.1 Location and orientation of the forest-tundra

The circumpolar forest-tundra corresponds broadly to zones of confluence of dominant air masses, and to relevant isorads and isotherms. In the subarctic NWT, relevant climatic and vegetation isolines show a clear NW--SE orientation. This orientation likely results from the interaction of the polar gradient in global solar radiation with the west to east weakening of Pacific air influence (attributable in large part to the Cordilleran barrier).

Pacific airstreams moderate the spring climate first in the west and later extend inland as a wedge of warm, relatively moist air. Arctic air is supplanted from SW to NE. The west to east march of spring is driven not only by proximity to Pacific source regions but also by the vegetation and snow cover. Low spring albedos of closed crown forest (0.1-0.3) contrast sharply with those of snow-covered tundra (0.7-0.8). Deep and long-lying snow in northern Manitoba and southern Keewatin further slows the replacement of Arctic air by Pacific air.

6.2.2 Width of the forest-tundra

The subarctic forest-tundra of the NWT, as delimited by the northern limit of trees 3-4 m tall and the southern limit of upland tundra, spans an average 150 ± 75 km and increases in width from northwest to southeast. This widening of the forest-tundra is most evident between the East Arm of Great Slave Lake and eastern Keewatin; greatest widths are encountered between the Dubawnt River and eastern Manitoba--Keewatin at 235-345 km.

While vegetation and climatic gradients correlate fairly well, synoptic climate cannot fully account for the great width of the forest-tundra in the southeast and the steep transition in many places elsewhere. Topoclimatic and edaphic factors may help to account for both the width of the forest-tundra and the location of steep vegetation gradients within it.

Regional slope of the land probably accounts for much of the variation in the width of the forest-tundra. North of Dease Arm, Great Bear Lake, and in the central district from the Snare River SE to the East Arm of Great Slave Lake, elevations rise from south to north or SW to NE, parallel to the vegetation gradient. Evidently a strong topoclimatic gradient is created by the northward rise of elevation, eliciting steep vegetation gradients. Conversely, the NE fall of elevation between the East Arm and eastern Keewatin--Manitoba is likely instrumental in helping to account for a wide forest-tundra, and for the northward extension of trees in the Thelon River area.

6.2.3 Cover structure of dominant forest-tundra vegetation

Gradual change at both high and low cover values and steep gradients between about 5-85% cover are approximated by a sigmoid curve. The sigmoid cover pattern appears to be a fundamental characteristic of spatial vegetation change in the forest-tundra. The mathematical (not necessarily geographic) core of the cover gradient, within which the tree:upland tundra cover ratio changes from 10:1 to 1:10, ranges in width from 25-55% of the forest-tundra. The tails of the gradient, where tree:upland tundra cover is $>100:1$ or $<1:100$, span about 10% of the forest-tundra.

6.2.4 Climate and vegetation in regional perspective

A cardinal anomaly exists in the radiation budget of the forest-tundra of the NWT: the northwest functions on roughly 3/4 the mean annual net radiation available to central and southeast districts. Crossover of vegetation and radiation contours occurs in the central district north of Great Slave Lake. Other relevant isotherms and isorads show a similar diagonal orientation with vegetation contours. This vegetation--climate crossover coincides with a major landscape transition from sedimentary rocks overlain by fine-textured soils in the northwest to crystalline rocks overlain by coarse-textured soils on the Shield. Seven regional vegetation--synoptic climate anomalies are also discernible.

Highlands account for most southern outliers of forest-tundra in the northwest, e.g., the Colville Hills (peaks >600 m ASL, lying >300 m above the plain). High elevations probably also account for southern extensions of low arctic, e.g., south of the Dismal Lakes. Northward rise of elevation is correlated with a narrow forest-tundra, and NE fall of elevation correlated with the great breadth of the forest-tundra in the southeast.

6.2.4.1 Radiation budget

Lower temperatures and lower absorbed solar and net radiation values are characteristic of the forest-tundra of the northwest. For example, the northwest receives an average 15 kly mean annual net radiation as compared to 20 kly in the southeast. The southern portion of the forest-tundra across much of the central district is anomalously warm.

A lower cardinal temperature of 15 C has been shown important in determining the timing and success of seed germination in black spruce, and this may explain the absence of black spruce across much of the forest-tundra of the northwest. The northern limits of both black and white spruce on the Shield lie climatically south of their respective northwestern limits, indicative of edaphic controls.

6.2.4.2 Edaphic controls

Edaphic restriction or compensation may not only help to explain the cardinal climatic anomaly of the forest-tundra, but also the relative locations of steep vegetation gradients within the transition zone and its general increase in width from northwest to southeast.

On the relatively rich loamy soils of the northwest, the forest-tundra transition is narrow and located far north, as many sites retain trees till climatic thresholds are reached. Conversely, on the generally poor but heterogeneous terrain of the Shield, steep gradients in tree and upland tundra cover take place in the southern forest-tundra, with a patchwork of sites retaining trees well to the north (Plate 11). Here the forest-tundra is broad and lies, for the most part, climatically south of its potential. Similarly, the forest-tundra of the USSR is broadest ($\sim 100 \pm 60$ km S.D.) where it lies "south" of its climatic potential.

There appears sufficient evidence to conclude that (a) the poor sandy soils of the Shield contribute to a wide forest-tundra which lies for the greater part south of its climatic potential; (b) the higher quality loamy soils of the northwest contribute to a narrow forest-tundra which extends well north till climatic thresholds are reached; (c) edaphic restriction contributes to an eastern forest-tundra vegetation pattern, in which steep gradients in upland tundra and tree cover occur in the southern forest-tundra; and (d)

edaphic compensation contributes to a western forest-tundra pattern, in which steep vegetation gradients typically take place at the northern limit of the forest-tundra.

6.2.4.3 McTavish Arm, Great Bear Lake to east of the Coppermine River

High tree cover in this area may be correlated both with lower elevations and soils underlain by sedimentary rocks. Elevations rise eastward from Great Bear Lake to a plateau west of the Coppermine River, then fall at the valley of the Coppermine. Coincident with the elevation gradient is a transition from Archean crystalline rocks east of McTavish Arm to sediments and metasediments in the Coppermine River region. Low elevations and rich loamy soils in the Coppermine River region likely permit a high cover of trees. The rise in elevation and return to a band of acidic crystalline rocks east of the Coppermine River may combine to eliminate trees from the landscape.

6.2.4.4 Snare to Rocknest Lakes

Tree and upland tundra patterns in the Snare to Rocknest--Point Lakes region correlate with elevation and parent material changes. Trees decrease to zero cover on the plateau between Snare and Rocknest--Point Lakes, followed by a sharp rise in tree cover which coincides with a combined fall in elevation and a transition from

sandy brunisols over Archean gneisses to rich silt loams overlying mainly sediments and metasediments.

6.2.4.5 Thelon River

The fact that peak tree cover (10-20%) along the Thelon valley occupies an "island" from north of 64°N to upstream of the Ursus Islands suggests these tree stands are relictual outliers, but evidence for this is lacking. Tall trees with spire-like crowns indicate vigorous growth rates in many stands. Black spruce and larch occur along with the dominant white spruce, and large numbers of seedlings have been reported in many stands. Tree stands on the Thelon and its tributaries, at least in the absence of disturbance, presently seem capable of maintenance and even expansion in area.

Alluvial soils may contribute to the good growth of trees in the Thelon area. The heaviest forests occur on alluvium, grading upward into forest-tundra on the gentle valley slopes of the Thelon and elsewhere.

Northward fall of elevation may compensate at least partly for latitude. Mean elevation of the Thelon north of 64°N is 220 m lower, and average minimum elevation is 250 m lower, than in its upper reaches. By lapse rate alone the northward fall in elevation translates to a temperature difference of +1.8-2.0 C. In the main "island" of trees and tall shrubs along the middle Thelon, mean tree cover is 14% and shrubland cover is 6%. Thus 20% of the landscape has a relatively low albedo and a rough surface capable of lodging snow

and decreasing wind. Runnels are common in the area indicating well-watered slopes and perhaps finer soil texture than those of red till.

6.2.4.6 Great Slave Lake to eastern Keewatin--Manitoba

While much of the northern forest-tundra in this region has been considered relictual (see 6.1), there are difficulties with this view. An alternate interpretation of the great breadth of the eastern forest-tundra involves edaphic controls and the NE fall of elevation.

Edaphic restrictions may elicit steep gradients in vegetation cover in the southern forest-tundra, with low tree cover extending northward, perhaps in the mosaic of higher quality sites, till climatic thresholds are approached, resulting in a wide transition zone.

On average, elevations fall 100-150 m from SW to NE, which corresponds to a compensatory summer warming of -0.8 - 1.2 C, and perhaps contributes to the gradual vegetation gradients.

An exception to the NE fall of elevation provides further indication of topoclimatic effects: the highland between Nueltin Lake and the Watterson--Hicks Lakes area is characterized by depressed tree cover.

6.2.4.7 Kamilukuak Lake to Kazan River

High tree (mean 8%) and shrubland cover (mean 7%) may be due in part to the abundance of well-watered sites (e.g., drainages, slopes and slope bases, shores, low-lying areas and depressions). Combined tree and shrubland cover in the core area ranges from 20-45%; thus bioclimatic feedback may contribute to render the local climate more suitable for forest and shrubland than would appear from the synoptic level.

The land slopes to the NE, falling about 60-100 m in about 80 km, which perhaps contributes to the high tree cover.

6.2.4.8 Nueltin--Hicks--Henik Lakes region

In the region as a whole, low tree cover is associated with granites and crystalline gneisses and higher tree cover with sediments, metasediments, and basic volcanics.

In the Nueltin Lake area, bedrock changes are correlated with elevation gradients such that highlands are underlain by Archean granites while lower elevations are underlain by Archean crystalline gneisses, sediments, metasediments, and basic volcanics. In this area tree contours roughly parallel those of elevation and bedrock; tree cover falls below 2% near the 300 m contour and transition to granite bedrock.

Elevations fall >150 m from east of Nueltin--Watterson Lakes to east of the Henik Lakes, corresponding to a compensatory summer

warming of ~ 1.2 C across 110-120 km. Runnels and slopewash are abundant in the area indicating extensive well-watered slopes.

6.2.4.9 SE Keewatin and NE Manitoba

East of 96°W , the limit of trees drops abruptly SSE along a line that lies between the 150-75 m contours in SE Keewatin, and reaches the shore of Hudson Bay a short distance north of the Caribou River, northern Manitoba. The landscape transition from uplands to poorly-drained lowlands and organic terrain depresses potential upland tundra cover by preemption, and probably contributes to low tree cover also.

The distance to which cold moist marine air extends inland is an open question. The 10°C mean July air isotherm plunges south upon reaching Hudson Bay, as does the 60 day contour for frost-free period. Such a deterioration of the growing season may be important, but it is noteworthy that much of the forest-tundra of the northwest experiences an even shorter frost-free period.

6.3 Tree and tundra landscape patterns at the extremes of the forest-tundra

Neither summer warmth nor physical protection from winter desiccation appear to be factors in the wet mineral soil--tree outlier landscape pattern. Soils in outlier stands are wetter than the

surrounding upland tundra soils and tend towards thicker moss and organic mats. Compared to dry coarse-textured soils, wet fine-textured soils freeze slower in the fall, which may prolong the hardening period, thus ensuring better resistance to winter frost and desiccation. Conversely, slower spring thawing of wet, insulated soils might safeguard against premature breaking of dormancy.

The landscape pattern may also be related to more successful sexual and asexual reproduction than is possible on dry soils. While growing conditions for adult trees are not conducive to rapid growth on wet and summer-cold soils, conditions for seed reproduction and cloning seem favorable. Factors favoring vigorous tree growth are evidently not those that favor good reproduction.

The treelessness of dry sites at the southern limit of the forest-tundra may result from physiological stresses to seedlings during germination and establishment, brought on by droughty conditions, wide fluctuations in soil temperatures, and perhaps to inadequate snow cover. Such conditions might manifest themselves in poor resistance to frost and desiccation.

The initiation of persistent treeless ground on fire-prone uplands in the study region deserves further research.

6.4 Areal pattern of burn in the subarctic NWT

The complex areal pattern of burn in the subarctic NWT is understandable with reference to weather, terrain influences, and regeneration rates.

Burns show a general decrease in cover from the far northwest to the southeast, while cover of water bodies increases from northwest to southeast. The role of lakes acting as firebreaks or in locally modifying summer weather deserves further attention.

In the northwest, weather presents low to very low fire risk and cannot account for the observed burn pattern. The uniformity of the flat till plains, high cover of mature forest, and scarcity of lakes, coupled with dominance of poorly-regenerating white spruce (in the forest-tundra), are likely primary factors accounting for the extensive burned terrain.

In the eastern half of the study region, the northern burn limit normally does not extend beyond the line where tree cover equals upland tundra cover. In this region, tree cover usually drops rapidly within the southern half of the forest-tundra, constraining burn to low cover values. Burns extend about 25-75 km into the forest-tundra, reaching ever lower cover with distance east of Great Slave Lake. Burn cover in the forest-tundra north of Great Slave Lake generally exceeds that east of Great Slave Lake. Lower fire weather risk and an abundance of lakes may account for the lower cover of treeless burn both in the open crown and forest-tundra regions east of Great Slave Lake.

Treeless burns north of Great Slave Lake peak in cover in the low subarctic along a NW--SE axis which lies NE of high fire risk and occurrence zones. Higher fire occurrence southward, offset by longer recovery time northward, may account for this pattern.

6.5 The sigmoid cover structure of the forest-tundra in relation to environmental factors

An integrated system of climate and landscape is indicated by the observed recurrent patterns in vegetation cover. Climate is linked with the landscape through features such as albedo, aerodynamic roughness, and depth and duration of snowcover.

In the steep phase of the vegetation cover gradient, positive feedbacks between vegetation, climate, and snowcover may drive the landscape to either tree or tundra dominance. The sigmoid cover structure of the forest-tundra might be viewed as the integral of landscape--climate feedbacks, edaphic and fire influences, and vegetation response rate in an environment marginal for both forest and tundra vegetation.

Forest bioclimatic feedbacks, rapid post-fire regeneration, and edaphic compensation might act to maximize tree cover in space or time; steep cover gradients would occur near the climatic threshold for tree growth. Tundra bioclimatic feedbacks, failure of tree regeneration, and edaphic restrictions might induce steep cover gradients south of the climatic potential for trees, resulting in a broad (spatial) or persistent (temporal) tundra-dominated zone and a narrow or transient forest-dominated zone.

6.6 Distribution of selected patterned ground features

Peatland polygons show the widest distribution of any of the

patterned ground features assessed. High center peat polygons predominate in the forest-tundra and southward through the low subarctic. In the northern forest-tundra, low center polygons appear and become regionally prominent in the low arctic, such as on Tuktoyaktuk Peninsula.

Although nearly ubiquitous, high center peat polygons reach their greatest prominence in a band spanning the northern portion of the low subarctic and the southern portion of the forest-tundra. Treeless peat plateaus are the predominant landform exhibiting high center pattern in the study region.

Soils with slow percolation and shallow active layers favor surface flow of water. On the fine-textured soils of the northwest, elongate slope pattern (runnels) extends from the low arctic southward through the low subarctic. The sandy soils of the Shield favor subsurface flow of water and are not conducive to runnel formation. In the Mackenzie district, elongate slope forms (runnels and stripes) are conspicuous in the low arctic and rare in the forest-tundra, thus making them a good indicator of the northern limit of the high subarctic. In Keewatin, elongate slope features extend somewhat farther south into the forest-tundra.

The southern limit of conspicuous upland patterned ground provides a good indicator of the southern limit of the forest-tundra across much of the study region. The chief exception lies in the northwest where earth hummocks extend southward through the low subarctic on perennially frozen loamy soils. Mudboils are conspicuous in well- to imperfectly-drained tundras and forest-tundras of the Shield; as active features they do not extend south of the forest-tundra. Frost

cracks, typically in the form of polygons, extend from the low arctic through the high subarctic on coarse-textured soils, usually in tundra, rarely in forest-tundra communities. Trees are usually absent from polygonally patterned uplands, due most likely to the dry conditions of coarse-textured soils.

Patterned ground in lake shallows occurs commonly in the forest-tundra and abundantly in the low arctic. With the exception of the northwest, where fine-textured parent materials predominate and lakes are few, the southern limit of lake shallow pattern is an excellent indicator of the southern limit of the forest-tundra.

6.7 Forest-tundra vegetation communities and species groups in overview

Within the forest-tundra, it appears that soil moisture is the prime determinant of physiognomic vegetation types (e.g., lichen, graminoid, dwarf shrub, medium and tall shrub, tree); i.e., physiognomy is independent of soil pH. In contrast, plant associations are correlated with both pH and moisture.

Mesic soils in the forest-tundra support medium shrub tundras (dominant northward) and tree communities (dominant southward). Forests of single-stemmed trees undergo a transition northward to woodlands, forest-tundras (widely-spaced, typically clonal spruce in a tundra matrix), and thickets in which clonal reproduction is prominent.

The black spruce/dwarf birch/ericad/lichen association dominates

acidic loamy sand and sandy loam tills of the Shield in the southern portion of the forest-tundra. Northward, dwarf birch--willow/ericad/lichen dominates mesic acidic soils.

On basic loamy soils of the northwest, forest and forest-tundra stands are dominated by white spruce/dwarf birch--willow/*Dryas*--legumes/*Carex*/moss (non-calcareous silt loams in the northwest support a white spruce/shrub/moss association). Basic tundras support a diversity of plant associations, but the core type is the medium shrub/ *Dryas*- -legumes- *Arctostaphylos rubra*/ *Carex*/ lichen association on wet-mesic sites, with a decline in medium shrubs on mesic and dry-mesic soils.

A discontinuity between southeastern and northwestern species, indicative of edaphic and geographic components in the vegetation, occurs near the Shield/sedimentary terrain boundary north of Great Slave Lake. This discontinuity coincides with a marked change in the orientation of vegetation cover contours. At the crystalline rocks of the Shield, the forest-tundra drops precipitously southward. The prominence of arctic--alpine species in the northwest, and of low subarctic species in the southeast, highlights the disparate climates within the forest-tundra. An analagous discontinuity in species composition and abundance occurs at the Shield/Paleozoic boundary in the forests of the low boreal region in central Canada.

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Appendix 1. Key to physiognomic vegetation types of the subarctic for use with black and white airphotos of 1:50,000 to 1:70,000 scale.

Tonal grey scale values are given as a rough approximation, as vegetation tones vary with photographic conditions. In general, tree communities present the darkest tones, tall shrubs medium tones, and upland tundras the lightest tones. Tones of treeless wetlands vary greatly.

Differentiation beyond broad tundra communities, using non-stereo black and white airphotos at 1:50,000 scale is usually unreliable (Mackay 1958; this study). Locally, upland tundra communities may be split into various types, such as dwarf birch/ericad or *Dryas integrifolia*/*Carex rupestris*/*Cetraria*. Identification to this level usually requires ground truth, and is beyond the scope of the study.

Wetlands exhibit many forms such as bogs proper, palsas, treed peat plateaus, treeless, polygonal, and rilled and eroding peat plateaus, peat polygon areas, and bog mounds, and *Carex-Eriophorum*/brown moss meadows. These bog and fen types not only intergrade, but bog-fen wetland complexes are common.

Alnus crispa, *Betula glandulosa*, and *Salix* dominated communities in the forest-tundra typically occupy drainage lines, shore, and wet slopes. Shrublands are usually restricted to wet to moist sites, and may be visually transitional to other vegetation types on small scale black and white airphotos.

For example, short trees in drainage lines often cannot be distinguished from tall shrubs, and short trees and shrubs on a peat plateau comprise a community that is neither a tree community nor a treeless wetland tundra; and for lack of a better category are placed under shrub. Similarly, dark-toned grainy textured moist slopes may either be upland tundra or tall shrub, and burn-induced tall shrub is widespread in the northwest.

Thus, shrub is a heterogeneous category including plant communities that do not fit into the more easily defined tree, upland tundra and wetland communities.

Burned lands fall into three main types: trees (common), peat plateaus (occasional), and upland tundra (rare). Their identification on airphotos requires comparison with adjoining unburned types. Only freshly-burned trees were placed in a separate category; burned peatlands and upland tundra were included under their respective types. Most difficult to discern are burned upland tundras of the northwest. Here, reference to pre- and post-fire photos, or to low level (large scale) photos or ground truth are usually needed. The most obvious difference is a change from light to medium grey. Burn lines are often present.

Burned peat plateaus are easy to discern from unburned peatlands: light-toned *Cladonia*-covered peat plateaus contrast sharply with dark-toned exposed peats and shrubs.

Burns of sparsely treed communities are typically darker-toned

than adjoining unburned areas. This is especially true in the northwest where lichens are replaced after fire with darker-toned shrubs. In what were densely treed stands, fresh burns are characterized by a lighter tone, and a change from stippled to grainy texture. Ideally, burn lines show a sharp transition from unburned to burned communities. Lacking clear tonal and textural differences and burn lines, comparison of suspected burned terrain with that on islands and peninsulas is often helpful.

Forests over bedrock are typically sparse. When burned, trees and matrix vegetation may be consumed, resulting in lighter tones if the matrix was shrubby, or in darker tones if the matrix was lichen dominated. In most cases, the harsher textures of the bedrock show through after the burn. Along the Shield--Paleozoic border between Great Bear and Great Slave Lakes, the differentiation between burns and rockland can be difficult.

Tree communities can usually be distinguished as to closed crown, open crown (scattered individuals), or clumped types. These types intergrade, however, and are controlled primarily by quantity and distribution of available water. Moreover, a stand can display various levels of pattern, such as widely scattered clones of clumped aerial stems, or a clumped distribution of clones. These differences in tree density and distribution show a regional trend: closely-spaced individual trees in the high and mid-boreal region (closed crown forest); widely scattered individuals in the low subarctic (open crown forest); and irregularly distributed clones in the high subarctic (forest-tundra). But tree density and pattern are extremely variable within a region; moisture regime, topography, aspect, depth to bedrock, and other site-related factors are strong regulators of density and pattern. The regional trends are presumably due to climate and are weakly expressed. The difficulty of categorizing tree communities as to pattern and density resulted in the use of a simple "tree" category.

-
- 1A. SURFACE STIPPLED; USUALLY DARK; SOMETIMES WITH TREE SHADOWS;
GO TO 2.
 - 1B. SURFACE NOT STIPPLED; OFTEN MONOTONAL; TREELESS; GO TO 4.
 - 2A. STIPPLING REGULAR, CLOSE, FINE, WITH DARK GREY TONE (N4-5);
INDIVIDUAL TREES BARELY DISCERNIBLE; MESIC TO WET-MESIC
SITES:.....CLOSED CROWN FOREST
 - 2B. NOT AS ABOVE; GO TO 3.
 - 3A. STIPPLING REGULAR, DARK TONE (N4-5); ON A LIGHTER GREY MATRIX
(N6-7), WITH SMOOTH TEXTURE; INDIVIDUAL TREES DISCERNIBLE,
WIDELY SCATTERED; DENSITY +/- CONSTANT; TYPICALLY DRY UPLANDS
OF THE LOW SUBARCTIC (OR RARELY TREED BOGS):
.....OPEN CROWN FOREST

- 3B. STIPPLING IRREGULAR AND SOMETIMES COARSE, DARK TONE (N4-5); MATRIX TONE USUALLY LIGHTER (N5-7), AND SMOOTH; DENSITY VARIABLE; INDIVIDUAL TREES NOT DISCERNIBLE; TREES TYPICALLY CLONAL; UPLANDS, SLOPES, LAKESHORES, DEPRESSIONS, DRAINAGES; TYPICALLY HIGH SUBARCTIC:.....CLIMPED TREES
- 4A. MEDIUM TO DARK TONE (N4-6); TEXTURE GRAINY TO VERY FINELY STIPPLED; DRAINAGES, SHORES, SNOWBED MARGINS, WET SLOPES, SOMETIMES MOIST UPLANDS; SHRUB FENS, THICKETS, SHRUBBY PEAT PLATEAUS AND BOGS (RARE); *Betula*, *Salix*, *Alnus crispa*; TRANSITIONAL TO TREELESS WETLAND, UPLAND TUNDRA, AND TREE COMMUNITIES; A WELL-WATERED COMMUNITY:.....TALL SHRUB
- 4B. TONE AND TEXTURE VARIABLE; WITH OR WITHOUT PATTERN; LOWLANDS OR UPLANDS; GO TO 5.
- 5A. MEDIUM TO LIGHT GREY (N5-7); TEXTURE SMOOTH, FEATURELESS, OR WITH POLYGONAL, CIRCULAR, OR NET PATTERN; DARKEST TONE WHEN COVERED WITH DARK LICHENS OR DENSE LOW SHRUBS IN MOIST TERRAIN; UPLANDS AND SLOPES:.....UPLAND TUNDRA
- 5B. IN BEDROCK-CONTROLLED LANDSCAPES ONLY: TONE LIGHTER AND TEXTURE ROUGHER THAN SURROUNDINGS; LITTLE OR NO OBVIOUS VEGETATION; BEDROCK UPLANDS:.....ROCKLAND
- 5C. MEDIUM TO VERY LIGHT GREY (N5-8); TEXTURE USUALLY SMOOTH, FEATURELESS OR WITH PEATLAND POLYGONS, OR LARGE FEATURED RIBS, NETS, ETC.; MAY BE PONDED; WET SLOPES AND DEPRESSIONS; GO TO 6:.....TREELESS WETLAND

Unlike shrub and upland communities, wetland types are often identifiable because they exhibit unique large scale ribbed or reticulate features, ponds of various shapes, polygons, rill features, and topographic position. The following key identifies some of the more common wetland types.

KEY TO AERIALY CONSPICUOUS WETLAND TYPES

- 6A. MEDIUM TONE (TO VERY LIGHT GREY WHEN LICHEN-COVERED); OFTEN POLYGONALLY PATTERNED; ROUNDED PONDS; OFTEN THERMOKARST FEATURES; SLOPES, DEPRESSIONS; BOREAL TO SUBARCTIC; INCLUDES PALSAS, PEAT PLATEAUS, PEAT MOUNDS (TO LOW ARCTIC AS PEAT POLYGON AREAS):.....OMBROTROPHIC WETLANDS
- 6B. TONE USUALLY LIGHT GREY, UNIFORM; TEXTURE SMOOTH; USUALLY LACKING POLYGONS; PONDS, IF PRESENT, ROUNDED TO ELONGATE; LOWLANDS AND DRAINAGE LINES; LIGHT TONED (N7) AND FEATURELESS AS WET MEADOWS; BOREAL TO LOW ARCTIC:..MINEROTROPHIC WETLANDS
- 6C. TONE VARIABLE; TEXTURE MOTTLED AND IRREGULAR; LACKING POLYGONS, BUT COMMONLY RIBBED OR NETTED; OFTEN SHOWING THERMOKARST FEATURES; PONDS IRREGULAR; LOWLANDS; CAN OCCUR AS BOG-FENS; LOW SUBARCTIC TO LOW ARCTIC:.....MIXED WETLANDS

Appendix 2. FORTRAN program used in adjusting vegetation cover percentages, decimalizing latitudes and longitudes, and performing a Lambert conformal map projection.

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C      This program takes raw airphoto data and adjusts the values
C      to percent of land surface.  Compiled with *FORTRANVS.
C      Variables:
C      TSTRIR = trees, without burn added, unadjusted for rockland
C      TSTRIC = trees, without burn added, adjusted for rockland
C      TR = trees plus burned trees, unadjusted for rockland
C      T = trees plus burned trees, adjusted for rockland
C      STU = shrubland, adjusted for rockland
C      WTU = treeless wetland, adjusted for rockland
C      UTU = upland tundra, adjusted for rockland
C      UTUR = upland tundra, unadjusted for rockland;
C              adjusting for rockland had little or no effect
C              on forest-tundra zonation since most rockland in the
C              study region lies south of the limit of upland tundra
C              or north of the limit of trees; UTUR was computed
C              to assess adjustment for rockland and is not depicted
C      TUTU = T/UTU RATIO, where 0.001 added to utu to prevent
C              dividing by zero (causing computer error);
C              in a separate program, TUTU is then log10 transformed
C              as follows: TUTU = LOG10 (TUTU+0.00001) + 3.0;
C              the addition of a small number to TUTU is needed to
C              prevent taking LOG10 of zero (causing computer error)
C      B = burned trees, unadjusted for rockland;
C              the small amounts of burned upland tundra and peat
C              plateaus are included under UTU and WTU
C      R = rockland
C      E = eroding terrain, unadj. for rockland (not depicted)
C      OT = snow cover (not depicted)
C      WTUBRD = STU + WTU
C      STUBRD = STU + B; this was assessed since burned areas are
C              often covered with tall shrubs after fire;
C              STUBRD approximates shrubland in a broad sense;
C      TUNDRA = STU + WTU + UTU
C      TLESS = UTU + STU + WTU + B + R
C              TLESS sums all treeless ground, without regard
C              to origin;
C      U = UNSUITABLE due to clouds, focus, overwriting, corner
C              tabs
C      W = WATER

C      For example, adjusted %T=(100T+B)/(raw sum - (u+w+r)).
C      The program also decimalizes the longitudes and latitudes.
C      Finally, with a call to LAMB, the longitudes and latitudes
C      are transformed to a Lambert Conformal map projection.

C      FUNCTION CORCAL (RAW, DENOM)
C      CORCAL = (100*RAW/DENOM)
C      RETURN
C      END

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INTEGER*4 RELIEF
DOUBLE PRECISION DLONG,DLAT,DNORTH,DEAST,DCM,DSPAR,DNPAR
CHARACTER*4 VEGR
CHARACTER*23 SNLROC
CHARACTER*125 LASTP
CHARACTER*15 IFIRST
10 READ(5,1,END=100)IFIRST, LONGD, LONGM, LONGS, LATD, LATM,
+LATS, VEGR, T, UTU, STU, WTU, E, R, W, B, U, OT, RAWSUM, SNLROC, MINELV,
+MAXELV, LASTP
1  FORMAT (A,2(I3,TR1,I2,TR1,I2,TR1),A,10(F4.1,TR1),F5.1,A,
+      2(I4,TR1),A)
CHKRAW=RAWSUM-(T+UTU+STU+WTU+E+R+W+B+U+OT)
150 IF(ABS(CHKRAW) .LT. 0.01) GO TO 15
WRITE(7,1)IFIRST, LONGD, LONGM, LONGS, LATD, LATM, LATS, VEGR, T,
+      UTU, STU, WTU, E, R, W, B, U, OT, RAWSUM, LASTP
GO TO 10
15 DENOMA=RAWSUM - (U+W+R+OT)
DENOMB=RAWSUM - (U+W+OT)
DENOMC=RAWSUM - (W)
TLESS = CORCAL ((UTU+STU+WTU+R+B+TUN), DENOMB)
TSTRIC = CORCAL (T, DENOMA)
TSTRIR = CORCAL (T, DENOMB)
TR = CORCAL ((T+B), DENOMB)
T = CORCAL ((T+B), DENOMA)
UTUBRD = CORCAL ((UTU + R),DENOMB)
UTUR = CORCAL (UTU, DENOMB)
UTU = CORCAL (UTU, DENOMA)
TUTU = T/(UTU + 0.001)
STU = CORCAL (STU, DENOMA)
WTU = CORCAL (WTU, DENOMA)
WTUBRD = WTU + STU
TUNDRA = UTU + STU + WTU
B = CORCAL (B, DENOMB)
STUBRD = STU + B
R = CORCAL (R, DENOMB)
E = CORCAL (E, DENOMB)
OT = CORCAL (OT,DENOMC)
C RELIEF is the local relief across an airphoto:
C it equals maximum elevation - minimum elevation
C RELIEF = MAXELV - MINELV

DLONG=LONGD+(LONGM/60.)+(LONGS/3600.)
DLAT=LATD+(LATM/60.)+(LATS/3600.)
DCM=114.75
DNPAR=67.00
DSPAR=61.00
CALL LAMB(DLAT,DLONG,DNORTH,DEAST;DCM,DSPAR,DNPAR)
PRINT 2,IFIRST,DEAST,DNORTH,VEGR,T,TSTRIC,UTU,TUTU,STU,
+      WTU,E,R,W,B,U,OT,UTUBRD,STUBRD,WTUBRD,TUNDRA,
+      TLESS,RAWSUM,SNLROC,MINELV,MAXELV,RELIEF,TR,
+      TSTRIR,UTUR,LASTP
2  FORMAT (A,F11.0,TR1,F13.0,TR1,A,2(F5.1,TR1),F4.1,TR1,F11.5,
+      TR1,9(F4.1,TR1),5(F5.1,TR1),A,3(I4,TR1),3(F5.1,TR1),
+      A)

```